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Vernalization and photoperiodism of winter wheat

John Frederick Ahrens
Iowa State College

VERNALIZATION AND PHOTOPERIODISM OF WINTER WHEAT

by

John Frederick Ahrens

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Signature was redacted for privacy.
In Charge of Major Work

Signature was redacted for privacy.
Head of Major Department

Signature was redacted for privacy.
Dean of Graduate College

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INTRODUCTION

Vernalization and photoperiodism are two phenomena of utmost importance in the regulation of flowering in higher plants. Vernalization refers to the flower-inducing effects of cool temperature and, as a process, has come to mean the cool-temperature treatment of either seeds, bulbs, or plants for the purpose of accelerating flowering. Photoperiodism, on the other hand, is the flowering response of plants to length of day or photoperiod. Plants have been classified according to their flowering responses to optimal photoperiods as short-day, long-day, intermediate-day, or indeterminate (29, 30).

The flowering plants as a whole also can be grouped as annuals, biennials or perennials according to the time required for completion of their life cycles in natural habitats. In the annuals the change from vegetative to floral state is mediated largely by photoperiodic reactions, while in the biennials and perennials a period of cool temperature also is required for flowering. The winter cereals fit into a specific group of biennials which are customarily planted in the fall and flower the following spring. They are a most intriguing group from the standpoint of floral development because they are responsive to both vernalization and photoperiod, but eventually flower under a wide range of temperature and photoperiod conditions. It is in this group that

the interactions of cool temperature and photoperiod become very important.

Numerous studies have indicated the presence of three major phases in floral development: induction, initiation, and further floral development. Induction has been defined as a chemical or hormonal differentiation resulting in the initiation of floral primordia while initiation is the phase in which there is a morphological change in the vegetative meristem and visible floral primordia are produced. Further floral development refers to the growth and development of the floral primordia leading to mature flowers and fruit. The temperature and photoperiod optima may differ for the three phases.

The present study was undertaken with winter wheat for the purpose of clarifying its response to vernalization and photoperiod in the three phases of development described above. A previous study by the writer (2) had indicated that under certain conditions winter wheat did not behave as a "short-day⟶long-day" plant as McKinney and Sando (59) had concluded. In addition, evidence was obtained from the literature that auxins act in reducing the requirement for cool temperature in certain plants. Several chemicals were tested, therefore, in attempts to alter the induction phase of winter wheat.

REVIEW OF LITERATURE

There are numerous detailed reviews of past research on vernalization and photoperiodism. Bulletin No. 17 of the Imperial Bureaux of Plant Genetics entitled, "Vernalization and phasic development of plants" (44), has extensive references to the earlier work, while Murneek and Whyte (60) and Gregory (33, 34) have made more recent reviews of the field. Recent reviews also have been made by Leopold (48), Thompson (72), Bonner and Liverman (6), and Naylor (61). Because of the immensity of the literature in this area, the present review will be somewhat limited in its scope.

The importance of effects of light and temperature on the flowering responses of plants has been recognized for some time. Klebs, as reported by Purvis (67), was one of the first to observe that light and temperature effects were critical at different times in plant development. In his work with Sempervivum Klebs reportedly recognized three stages in the flowering process: (a) the production of a condition of "ripeness to flower" which was obtained under low temperatures and low light intensity, (b) the formation of macroscopic flower primordia, and (c) the further development of floral structures. The production of a condition of "ripeness to flower" has become known as induction and has been defined as a chemical or hormonal differentiation resulting in the initiation of floral primordia (28). The second stage is the visible

initiation of the flower primordia, and the third is referred to as further development. All plants necessarily proceed through these phases in the production of mature flowers and fruit, although different plants will vary in their optimum environments for the completion of each phase. In this review and throughout the manuscript these three phases and their interactions are considered in winter wheat and related plants.

Induction

Induction can be broken down into two more or less distinct types. Annual plants requiring no low temperature for flowering are induced by photoperiodic stimuli, thus the term, photoperiodic induction. Winter annuals and biennials, however, while also requiring photoperiodic induction, must go through a period of low temperatures which may be referred to as thermo-induction or vernalization. Lysenko's theory of phasic development of the winter cereals, as reported by Whyte (74), held that the thermo-phase in winter wheat must be satisfied by low temperatures before flowering could occur. This has been shown to be in error by several workers (57, 67) who found that induction and flowering could eventually occur even at high temperatures throughout the life of the plant.. This does not mean that vernalization and photoperiodic induction are one and the same phenomenon, however, even though the end result of their interaction is the same -- the initiation of spikelet primordia. McKinney and Sando (59) and Purvis

(67) have shown that light is of no consequence in the vernalization of seeds of winter wheat and rye and that no acceleration of heading in these plants can be obtained by any photoperiodic induction treatment comparable to that produced by cool temperatures.

Vernalization

Vernalization, as previously mentioned, is the cool-temperature induction process in winter annuals and biennials. The term is derived from the Russian "jarovization" which means to make "spring-like" (56).

Most of the early work in vernalization of the small grains was done by the Russians, who at one time were reported to have had thousands of acres of wheat planted with vernalized seed (60). The advantage of its use would be in areas where severe winters ruin the fall-planted winter wheat. However, Martin (55) reported little or no practical application of seed vernalization in the United States where adapted spring varieties appear to be a better answer to these problems. Vernalization occurs naturally in fall-planted wheat and is of especial importance to wheat breeders who are interested in rapid plant increases.

In seed vernalization the seeds are first allowed to imbibe water up to 40 to 50 per cent by weight or until the radicles have just begun to break the seed coat. After germination has proceeded this far, the excess water is removed and

the seeds are transferred to cool temperatures (44). McKinney and Sando (59) have shown that high humidity is necessary to keep the moisture of the seeds above 40 per cent during vernalization. Allowing the seeds to dry out results in vernalization failure or devernalization.

Seeds must also be kept aerated during vernalization, as shown by several workers (36, 58). Gregory and Purvis (36) found that short periods of anaerobic conditions following vernalization resulted in a devernalization which could be corrected by vernalizing again in cool temperature with ample oxygen supply. Unlike vernalization in growing plants, the process in seeds occurs in the absence of light and daylength has been shown to be of no effect (59).

The temperature and duration of the vernalization treatment have also been shown to be of importance (39, 67). Optimal vernalization temperatures and durations appear to be dependent upon the specific crop and variety (76). With the winter cereals, temperatures just above freezing are most commonly used, both because of their effectiveness and the necessity of retarding growth of the seeds during the process. Hansel (39) has reported success in vernalization of Petkus rye at temperatures as low as -4° C., however. In doing this the seeds were exposed to increasingly lower temperatures, from 0° to the -4° C. over a 2-day period. The present writer (2) found that at temperatures of 34° F. in vernalizing seeds

and 45° F. in growing plants of Pawnee wheat, a minimum period of 3 to 4 weeks was required for any acceleration of heading under subsequent long photoperiods and warm temperatures.

The requirement of a minimum critical level of vernalization can be explained by the effects of high temperature in causing devernalization to occur. Purvis and Gregory (69) reported that devernalization of winter rye seeds by high temperatures (35° C.) decreases as the time or degree of vernalization increases. They have postulated a two-step reaction in vernalization, involving a thermo-labile and a thermostable intermediate to account for this phenomenon.

The most important effect of vernalization is the acceleration of flowering in certain plants. In many plants cool temperature is required for the completion of the floral induction phase regardless of other environmental conditions. This is true of orchard grass (28), bluegrass (65), garden beets and others (72). However, in many reported experiments, plants of the winter cereals eventually flowered under favorable growing conditions without any cool-temperature treatments (1, 2, 24, 42, 59, 67).

Other effects of vernalization on plant development are a reduction in the number of tillers formed and a decrease in the leaf number at which heading occurs (59, 67). McKinney and Sando (59) observed a minimum of seven leaves produced in vernalized Harvest Queen winter wheat and Purvis and Gregory (68) found essentially the same to be true in Petkus rye.

More recently Gott et al. (32) found as few as five leaves produced in fully vernalized Petkus winter rye and four of these were present in the seed after vernalization. The concept advanced by Purvis and Gregory (69) is that vernalization in winter rye acts in reducing the total number of leaves required for flowering to take place. When the leaf number at heading has been attained in the seedling, the plant is considered to be fully induced or in a condition of "ripeness to flower".

The receptor of the cool temperature stimulus has been shown to be located within the embryo of vernalizing seeds. Gregory and Purvis (35) and McKinney and Sando (59) have succeeded in vernalizing the excised embryos of winter rye and winter wheat.

Photoperiodic induction

Cajlachjan has been reported by several workers (37, 48) to have been the first to show that the photoperiodic stimulus is produced in the leaves and is translocated to the apical meristem. Khudairi and Hamner (45) have since shown that the stimulus moves out of the leaf of short-day Xanthium 2 to 4 hours after a long dark period. This was accomplished by leaving only one leaf on a plant and dissecting the leaves at varying times after the end of the dark period and then noting the flowering response of the bud on subsequent long days.

In long-day plants, photoperiodic induction is dependent upon the light period, whereas long dark periods have been shown to be essential for induction in short-day plants (61). Therefore, long-day plants may be induced in continuous light, a dark period not being essential. The researches of Borthwick, Parker, and Hendricks (9, 11) on the action spectrums for floral induction in short- and long-day plants have indicated the close similarity of the two types. The action spectrum for inhibition of flower initiation during a light-interrupted night of short-day plants corresponds very closely to the action spectrum for promotion of initiation of long-day plants. Two regions of maximum effectiveness were observed, one in the red from 6000 to 6800 A° and a second in the blue-violet from 4000 to 4400 A°. The region of minimum effectiveness was found to be at 4800 A°. More recently two of these workers (40) reported that infra-red light has an effect similar to darkness and that infra-red and red light periods essentially reverse the effects of one another. A common pigment for long- and short-day plants with a reversible shift from red to infra-red absorbing forms has been postulated.

The spring and vernalized winter grains have been found, almost without exception, to be photoinduced and flower most rapidly on long photoperiods (10, 13, 59, 67). Purvis (67) cites data of Rosumov in which a 7-day period of long photoperiods following planting of spring barley resulted in an

acceleration in heading of 10 days on subsequent short photoperiods. Increasing a short photoperiod pre-treatment from 10 to 25 days resulted in a constant number of long days remaining until heading. Gott, Gregory, and Purvis (32) weekly dissected vernalized plants of winter rye on continuous light, short days (10 hours) and long days (17 hours) and reported that initiation was first observed within 3 weeks on 17-hour days and continuous light but was delayed until 7 weeks on 10-hour days. Since the minimal leaf number was found in all plants as early as 2 weeks after planting, these workers assumed that induction had been complete at that stage but that initiation was delayed on short days thereafter. Chinoy (13) applied treatments of short and long photoperiods to seedlings of vernalized wheat, the treatments lasting 12 days. He reported that long photoperiods during this 12-day period favored earliest flowering and these photoperiod effects were not masked by any "post-photoinductive" treatments that followed.

Wort (76) reports an exception to the usual long-day response of winter grains after vernalization. Fulhio winter wheat vernalized for 36 days was accelerated 14 days by a 5-day dark period followed by continuous light compared to continuous light throughout. Exposure to darkness for periods longer than 10 days resulted in an increase in the total time to flower. It is probable that the seeds of Fulhio wheat were not fully vernalized at planting, for the heading time

under continuous illumination was about 75 days, whereas the spring wheat headed in a normal 35 to 40 days.

There are several reports of the promotive effects of short photoperiods during early growth of unvernalized winter rye and winter wheat (32, 42, 59, 67). McKinney and Sando (59) reported that 8 weeks of short days followed by long days favored earliest heading of Harvest Queen and Turkey wheats at high temperatures. Gott et al. (32) noted the same effect in Petkus winter rye except that continuous light was more inductive than 8- or 10-hour days, and 17-hour days were intermediate. They also found that a light interruption of the long dark period during photoinduction on 8-hour days produced the same relatively inhibitory effect as 17-hour days. Initiation started in 10 weeks on continuous light, 12 weeks on 10-hour days, and 15 weeks on 17-hour days. It is rather unusual that continuous light and short days had similar promotive effects and would tend to suggest that the means of promotion were by different reaction mechanisms.

Further evidence to support the effect of short photoperiods in photoperiodic induction in the small grains has been presented by Gott et al. (32), Hänsel (38), McKinney and Sando (59) and Purvis (67), who reported that the length of the spike and the number of spikelet primordia was increased by short-day exposures of plants from vernalized seeds. Hänsel (38), in growing vernalized rye on 8-hour photoperiods for periods of 0 to 22 weeks and then removing the plants to

16-hour photoperiods noted that the number of spikelets per ear increased from 19.2 on 16-hour photoperiods to 39.6 on 22 weeks of 8-hour photoperiods followed by 16-hour photoperiods until heading. The spike lengths also increased from 5.4 cm to 10.3 cm, or about double that on long photoperiods continuously. Gott et al. (32) also observed that the number of spikelets produced for a given growth rate of the apex of rye was three times greater in short days than in continuous light.

There is at least one report in the literature of the failure of short days to be more effective than longs days in the induction of unvernalized winter cereals. Cajlachjan is reported to have grown winter rye during summers which headed in 64 days on continuous light, in 72 days on normal days followed by continuous light and in 86 days under 10 hours followed by continuous light (44). Winter barley and wheat responded more slowly than rye to acceleration by continuous light.

Interactions of temperature and photoperiod in induction

In the case of annual plants requiring no vernalization treatments, cool temperatures often delay initiation and flowering. Borthwick, Parker and Heinze (10) reported a delay in the heading of Wintex barley by cool temperatures or short photoperiods during the seedling stage. Parker and Borthwick (64) also observed an inhibition of floral induction of Biloxi

soybeans by temperatures of 50° F. or lower during a 5-day induction period.

In other instances, however, especially in the grasses, the reactions involved in photoperiodic induction and vernalization may proceed together. Loehwing (52) has commented on researches with several plants in which the vernalization and photoinductive phases overlap. Peterson and Loomis (65) reported that Kentucky bluegrass required cool temperatures and short photoperiods for floral induction, although short photoperiods alone did not cause induction nor did cool temperatures and long photoperiods. In orchard grass, Gardner and Loomis (28) showed that, although both cool temperatures and short photoperiods were required for induction, the two factors could be applied separately, as long as short photoperiods preceded cool temperatures. A week of long days at warm temperatures destroyed the short-day effect before it could be stabilized by cool temperatures.

The results obtained by McKinney and Sando (59) with winter wheats are further evidence of the promotive effects of short days during vernalization of certain plants. They exposed plants of Harvest Queen winter wheat to photoperiods of 8, 12 to 14, and 16 to 17 hours for a period of 54 days at temperatures of 51° F. for the first 36 days and 59° F. for the remaining 18 days. The plants were then transferred to 18- to 19-hour photoperiods at 75° F. temperatures and allowed to head. The plants which had been on 8 hours headed in 88 days,

those on 12 to 14 hours in 95, and those on 16 to 17 hours in 114 days. On this basis they classified winter wheat as a plant which flowers earliest under short days and cool temperatures followed by long days and warm temperatures. However, this writer (2), in working with Pawnee winter wheat, obtained a variable heading response to 11-hour photoperiods at 45° F. for short vernalization periods of 3 to 4 weeks and no difference between 11- and 18-hour photoperiods during 6-week periods of vernalization. Gardner (27) also studied the effects of 10 different photoperiods on the cool temperature effects in Pawnee wheat and found no differences in the average flowering dates during subsequent warm temperatures. Federov (21) reported that winter rye and winter wheat plants exposed to different photoperiods during vernalization were accelerated in their entire floral development by continuous light during the vernalization period. Gott et al. (32) also found promotive effects of continuous light during vernalization.

Gott et al. (32) have demonstrated that the length of the photoperiodic induction period following seed vernalization is determined by the length of the vernalization period. This writer (2) obtained similar results with Pawnee wheat plants. In general, the longer the time of vernalization the shorter the required period of photoperiodic induction following and the lower the leaf number at heading.

Floral initiation

Initiation of floral primordia is that phase of floral development in which the vegetative meristem starts to produce microscopically visible floral primordia as a result of the chemical differentiation which occurred during the reception of the photoperiod and temperature stimuli; i.e., during induction. Barnard (4) and Bonnett (8) have adequately described the transition from the vegetative to the reproductive state in wheat. Bonnett (8) described the development of the wheat spike in two phases, (a) vegetative and (b) reproductive. During the vegetative phase the internodes of the stem remain short and only leaf initials are produced by the growing point. Tiller production takes place and the growing point elongates but remains smooth in outline, producing single-ridged leaf primordia. The beginning of the reproductive stage is evidenced by formation of double ridges, the upper member of which develops into the spikelet initial. Concurrent with spikelet development certain of the stem internodes elongate. Fall-planted wheat was noted to remain in the vegetative condition during the winter and to initiate primordia in the spring.

The initiation of other small grains is similar to that in wheat and also appears to be a phenomenon favored by long photoperiods. After initiation has started the upper member of the double ridge becomes a spikelet on favorable long days,

or as shown by Purvis (67) with rye, the effect of short days at this stage is to arrest spikelet development and allow the lower member to form a leaf. Initiation eventually proceeds again but it is somewhat delayed.

Gardner and Loomis (28) reported that initiation of floral primordia in orchard grass was arrested by 45 days of short days following induction. Upon removal to long photoperiods, however, initiation proceeded again. Peterson and Loomis (65) and Wiggans and Frey (75) obtained most rapid floral development under long photoperiods in Kentucky bluegrass and oats.

Further floral development

Further floral development is described as the growth and differentiation of flowers following initiation of the floral primordia. It is a phase of floral development which has been adequately studied by several workers but which has often been confounded with effects of the preceding stages. Garner and Allard's (29) grouping of plants according to the photoperiod range in which they flowered was essentially based on photoperiod effects on the further floral development phase. However, optimum photoperiods for further floral development are not necessarily optimum for the other phases of floral development.

Short photoperiods have been shown to be particularly inhibitory to further floral development in the northern grasses.

Peterson and Loomis (65) obtained 10 times as many heads on 15-hour photoperiods as on 11-hour photoperiods. Gardner and Loomis (28) obtained similar results with orchard grass which had initiated floral primordia before the start of the photoperiod treatments. Evans and Wilsie (20) and Gall (26) reported that long days favor the formation of more panicles of Bromus inermis. Olmstead (62, 63), in studying the photoperiod responses of 12 geographic strains of side-oats grama observed that internodal elongation and plant height were increasingly suppressed on 9-hour photoperiods with increase in the latitude of origin of the strains. The Texas clones flowered on 13-hour photoperiods and were suppressed on 15-hour photoperiods while the opposite was true of North Dakota clones. Zones of adaptation play a large part in the photoperiod response of a species or varieties of the same species.

Work with several of the cereal plants studied also indicates a long-day requirement for floral development. Wiggans and Frey (75) reported that no heads formed within 90 days in oats on 9- and 12-hour photoperiods. Borthwick, Parker, and Heinze (10) obtained delays in heading and absence of fertile seeds with Wintex barley on 12-hour days. Purvis (67) reported most rapid further development of Petkus rye on long photoperiods. Wort (76) observed that Marquis spring wheat headed as early on 8 hours as on 24 hours after 28 days of continuous illumination. Apparently photoperiod is not critical in the later phases of floral development of Marquis spring wheat.

In studying the growth of the floral apex of Petkus rye on long and short photoperiods following initiation, Gott, Gregory and Purvis (32) observed that no grand period of growth occurred in plants on 8- or 10-hour photoperiods. Further development was suppressed and although the number of spikelet primordia increased there also were more leaves produced in the labile primordia. These workers also observed that growth of the spike after initiation was independent of vernalization effects and was dependent upon daylength. In long days there was a marked grand period of growth; in short days there was only slow exponential rate of growth of the spike. Nitrogen applications also favored rapid spike growth as has been observed with other plants (28).

Several workers have reported abnormalities of heading on short photoperiods. Forster and Vasey (24) reported abnormal heading of winter wheats planted in the spring. Heads that had partially developed by fall often did not emerge. Forster et al. (23) transferred plants of wheat from long to 10- or 6-hour photoperiods and observed a retardation in stem elongation with either a delay or complete heading failure. Hurd-Karrer (42) made similar observations on Turkey winter wheat.

Several types of abnormalities may occur in the heads of wheat and other grasses developing on short photoperiods. Vegetative proliferation, which is the formation of leaves on

a floral axis, has been observed to occur in wheat and in other grasses as a result of marginal photoperiod treatments (25, 32, 70, 77). Wycherley (77) has suggested that the minimal requirement for flower hormone may be greater than that for culm initiation and that this higher level is not completely reached on short photoperiods and the plant reverts to vegetative habit. Gott, Gregory and Purvis (32) observed this partial reversion to vegetative growth with rye plants which had initiated floral primordia and were then removed to short photoperiods. Some of the characteristics they noted were: (a) leaves formed at lower ear internodes subtending spikelets, (b) lower spikelets may continue secondary growth, forming secondary ears, and (c) the lower internodes of the stem undergo extensive growth. None of these effects were observed in plants transferred from short to long photoperiods.

Modifying effects of chemicals

In 1942 Clark and Kerns (17) reported flower initiation of pineapple 2 months ahead of normal flowering by the application of ∝-naphthalene-acetic acid (NAA). Since that time much work has been directed toward the effects of auxins and anti-auxins on floral initiation and the relationships of these compounds with the proposed flowering hormone. Many varied results have been obtained but it is still only known that although auxin plays a part in flowering, depending upon

its concentration and time of application, it may be either inhibitory or promotive.

It is generally believed that low endogenous auxin concentrations promote flowering of short-day plants. Promotive effects on initiation of short-day plants by applying anti-auxins have been obtained by several workers including Fisher and Loomis (22) and Bonner and Thurlow (7). Vlitos and Meudt (73) caused flowering in short-day Maryland Monmouth tobacco plants exposed to long days by applying gamma radiation to the plants. Gordon (31) reported that such a treatment decreases the auxin content of the plant tissue treated.

Long-day plants have generally shown promotive responses to auxin applications. Leopold and Thiman (51) have obtained promotion of flowering of Wintex barley by applying low auxin concentrations. Hussey and Gregory (43) obtained no effects of such treatments on Petkus rye but confirmed Leopold and Thiman's observations on Wintex barley. These effects were said to be post-initiation effects, however. The present writer (2) noted the production of a larger number of heads and earlier heading as a result of NAA applications on unvernalized Minter wheat. The findings of Leopold (47) and Cooke (18) that more auxin is produced on long days than on short days would tend to strengthen the findings that higher auxin concentrations promote flowering in long-day plants. In a more recent finding, Hillman and Galston (41) obtained strong

inhibition of indoleacetic acid oxidase activity in buds of Alaska peas by exposure to red light. The inhibition was reversed by near infra-red radiation. The significance of this finding is that the red region of the spectrum is where maximum promotive effects have been obtained in initiation of long-day plants. The decreased indoleacetic acid oxidase activity may be important in allowing auxin to accumulate to the necessary level for induction.

There is current evidence that auxin or auxin-like compounds play a role in the vernalization process. Leopold and Guernsey (49, 50) treated Alaska peas and soybeans with NAA through a cut leaf at 25° C. and 10° C. and obtained promotion of flowering at the lower temperatures and inhibition at the higher. They referred to these promotive effects as "chemical vernalization". DeZeeuw and Leopold (19) reported shortening of the juvenile phase of brussel sprouts by auxin application during the cool temperature treatment. Gibberellic acid, a relatively recent compound which has many auxin-like properties, has shown some effects in reducing the vernalization requirement of certain plants. Lang (46) reported that daily applications of gibberellic acid caused initiation of certain carrot varieties and biennial Hyocyamus niger at warm temperatures but long days were still required for flower development. No promotive effects on flowering of Petkus winter rye were noted, however. Lona (53) obtained marked vegetative responses of winter wheat to gibberellic acid but the

cool temperature requirement was not replaced. Some floral promotion was noted at later stages of plant growth, although the most marked effect of the chemical was to greatly increase stem elongation and leaf growth. In time, however, chemical treatments may prove to be the answer to altering plant reproductive systems at will.

MATERIALS AND METHODS

Because of the many and varied experiments carried out, it appears desirable to present here only the experimental methods common to groups of experiments. The details of each individual experiment may then be found in the Experimental Results section.

General Techniques

Four varieties of Triticum aestivum L. were used as the experimental material. The Minter variety of winter wheat was employed in most experiments because it represents the northern winter wheat type. Pawnee, Harvest Queen, and Turkey were also used to compare differences in varieties and to compare with earlier results obtained by McKinney and Sando (59).

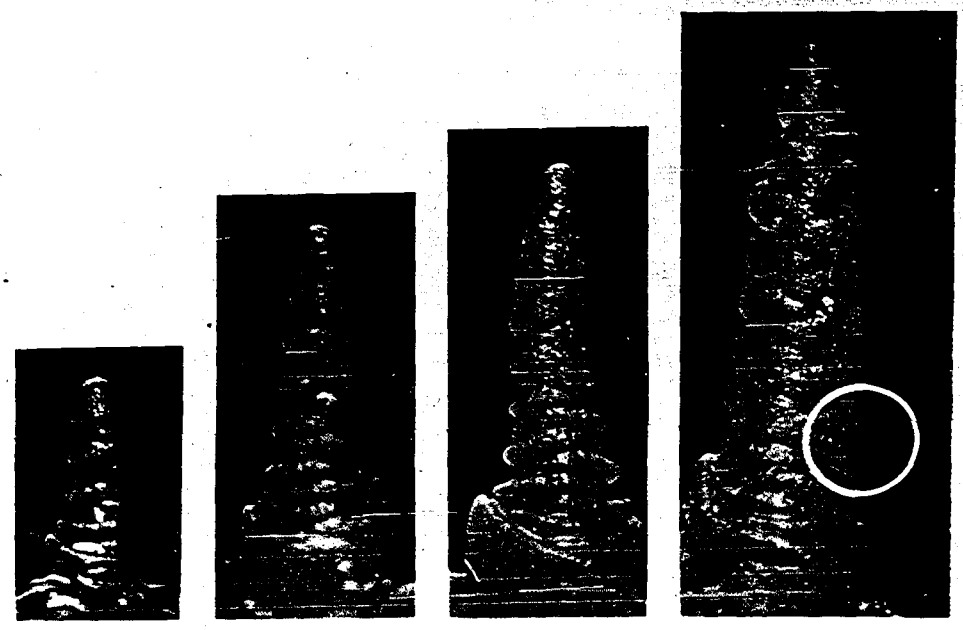
All experiments were carried out during the cooler months, starting in the fall of 1955 and continuing until the spring of 1957. Experiments 1 through 5 were conducted during the late fall of 1955 and the winter and spring of 1956 and Experiments 6 through 19 were conducted during the 1956-57 season. A sterilized, fertile loam soil and either 4-, 5-, or 6-inch pots were used in each experiment. Supplemental fertilizer in the form of 6-10-4 was added at intervals in Experiments 1 through 5 in order to maintain fertility. In the remaining experiments, however, after a single application of a teaspoon of the 6-10-4 fertilizer per pot, a nitrogen

solution was added at almost weekly intervals starting in most cases when the plants were less than 8 weeks of age.

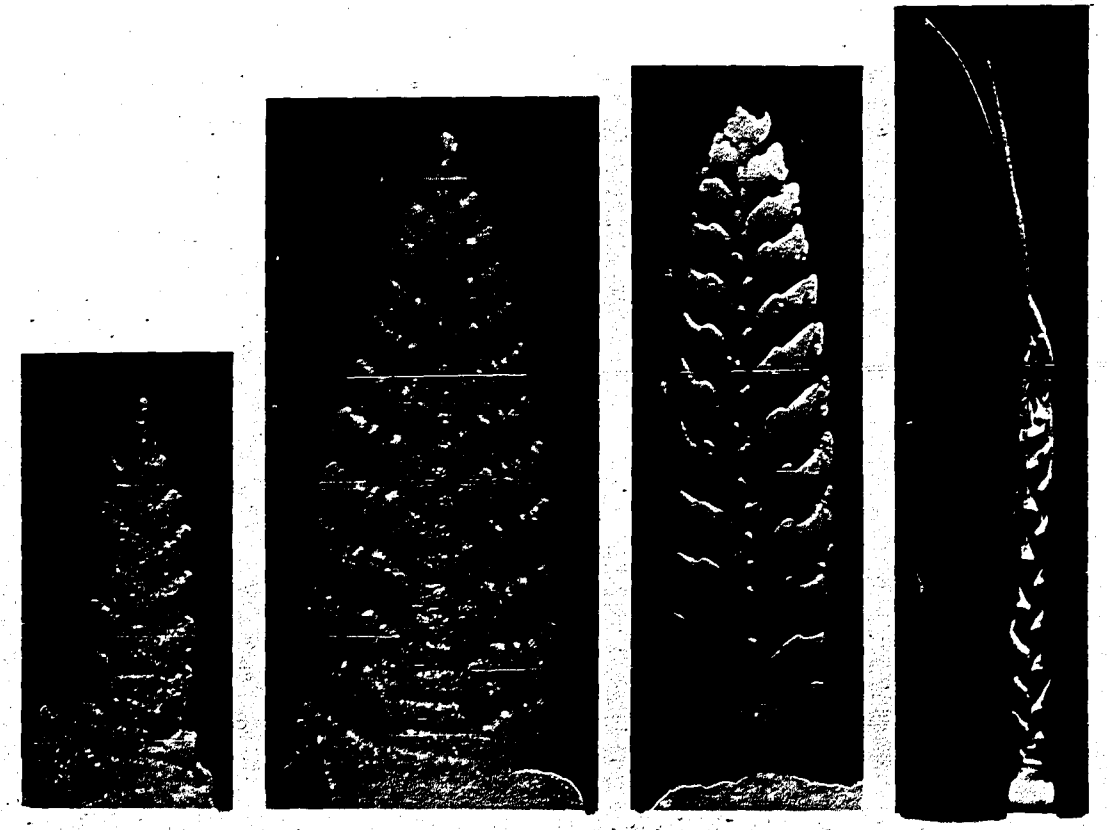
Measurements taken in the different experiments varied but can be grouped according to type. In certain experiments, plants were harvested at given times and measurements were made of the number of leaves, both visible and/or total, the number of tillers, the stage of development of the apex, the number of spikelet primordia and the length of the spike. The stages of development of the growing points were rather arbitrary but recognizable phases ranging in number from 1, which represents the vegetative condition, to 10, which represents the emerged spike. The stages from 1 to 8 are illustrated in Figure 1 and the descriptions of all stages are outlined in Table 1. The lengths of spikes were measured with an eyepiece micrometer mounted in the binocular microscope used in all dissection work. The measurement was made from the base of first proximal primordium which did not overlap the one above it.

In other cases plants were allowed to develop to maturity and the dates of awn emergence from the boot and sometimes the dates of first anther extrusion were noted. The lengths of the spikes at maturity were measured to the nearest millimeter with a millimeter scale, the measurements being made from the first proximal node of the spike to the end of the most distal lemma, exluding the awn. The number of spikelets per head were often counted, as was the total number of leaves.

Figure 1. Stages 1 to 8 of winter wheat development.
A - Stage 1, vegetative.
B - Stage 2, vegetative, elongate.
C - Stage 3, beginning of initiation.
D - Stage 4, primordia fused and double. Circle encloses double-ridged primordium. The upper ridge is a spikelet primordium and the lower is a leaf primordium.
E - Stage 5, primordia all fused.
F - Stage 6, lemmas and glumes visible.
G - Stage 7, floret primordia present, awns not exceeding tip of spikelet.
H - Stage 8, awns exceeding tip of spikelet.



A 70x B 70x C 70x D 70x



E 38x F 38x G 14x H 5x

Table 1. System of rating stage of development of apical meristem in wheat used during 1956-57 season

Stage	Approximate size range[a] (mm)	Description
1	0.2 - 0.6	vegetative, leaf primordia visible as alternate single ridges
2	0.6 - 0.9	vegetative, elongated spike, double ridges of spiklet primordia almost visible
3	0.8 - 1.3	double ridges clearly in evidence
4	1.1 - 1.5	ridges fused or rounded in mid-section and toward apex, double ridges still present at base
5	1.3 - 2.0	spikelet primordia all appearing as rounded protuberances, one or two primordial leaves may still be at base
6	1.8 - 2.4	glumes and lemmas clearly visible, no awns
7	2.2 - 8	floret primordia visible, lemmas not exceeding tip of spikelet
8	7 - 20	awns exceeding tip of spikelet
9	20 - 50	spike enclosed by only one leaf, in pre-emergence stages
10	50 -100	awns or tip of spike emerged from leaf sheath

[a]Spikes at the same stages often varied considerably in length, especially between different experiments.

Total leaf counts were made by counting the nodes above the coleoptile node or by counting the leaves themselves if all were still present. All measurements were made on the earliest tiller to head of each plant. In almost every case the plants were uniformly thinned to two per pot in the seedling stage, and the two values for a given measurement were averaged to obtain a single value for the experimental unit.

Temperature Treatments

Low temperature treatments were applied to either seeds or growing plants, depending upon the experiment. Where seeds were treated, approximately 35 ml of distilled water was added to 12 ml of seeds in a beaker and the seeds were allowed to soak at room temperature. When the radicles were first observed to break the seedcoat, usually after 14 to 18 hours, the excess water was drained off and the seeds were placed in the same beakers or in sterilized petri dishes. These, in turn, were placed in light-proof plastic containers and stored in a refrigerator at 1° C. to 2° C. or, in the case of Experiment 1, at -2° C. High humidity was maintained by placing wet paper towels at the bottom of the containers. The seeds were inspected at intervals and moistened if they appeared to be drying out. During these seed vernalization treatments, growth of the radicles continued slowly until at planting the radicles were often several inches and the

coleoptiles about 0.5 inches long, depending upon the length of the vernalization treatment.

With but two exceptions, the plant vernalization treatments were carried out in a cool greenhouse which was regulated by a combination of thermostat and vents to average weekly temperatures ranging from 40° to 48° F. The temperature remained fairly constant for both the 1956 and 1957 winters, although there was some daily and weekly variation. The average weekly temperatures were obtained by averaging hourly temperature values over weekly periods. All references to average weekly temperature will imply that this method of determination was used.

In Experiments 10 and 11, in order to achieve true replication of the cool temperatures, two cold frames were used for half of the plants. The frames were 2.5 feet deep and the standard 3 feet by 6 feet, width and length. A Kraft paper partition separated the two compartments which constituted different photoperiod treatments. These cold frames were thermostatically controlled to a minimum of 33° F. by heating coils but proved unsatisfactory in sub-zero weather and were subsequently discarded. The average weekly temperatures for the period of their use ranged from 30° to 37° F., although the day temperatures were often somewhat higher.

Specialized pieces of apparatus were also used in Experiments 4 and 5. In Experiment 5, two wooden box frames were obtained for the exposure of vernalized plants to high

temperatures. These were covered with a polyethylene plastic to allow light entry and one of the two units contained a 25-watt light bulb under an overturned pot. The bulb served to heat the chamber to 85° to 95° F. temperatures. The second chamber was an unheated control but the temperatures within were 5 to 10 degrees warmer than the greenhouse air on sunny days. The chambers, as shown in Figure 2, were situated on a greenhouse bench and exposed to 18-hour photoperiods with the supplementary incandescent illumination described earlier.

The two cardboard boxes illustrated in Figure 3 were used to heat the growing points of Minter wheat in Experiment 4 while exposing the leaves of the plants to low temperatures in the cool greenhouse. Again one of the two boxes was heated by a 25-watt light bulb which was wrapped with aluminum foil to exclude the light. This box was maintained at a temperature of 60° to 65° F. within, while the outside cool greenhouse temperature averaged 45° F. Four pots of two plants each were placed in the corners of each box and holes were punched in the sides of the boxes for leaves of each plant to protrude. The leaves were then started through the holes and cotton batting was lightly pressed in the remaining space of the holes of the heated box. The cotton was used to help maintain the higher inside temperature by preventing excessive heat loss.

The top covers of the box were kept tightly closed but the cracks were sufficiently large for air passage into the

Figure 2. Method used for testing effects of high temperature on vernalized plants.
Plastic covered chambers: (left) heated to 85° to 95° F., (right) unheated control at 75° to 85° F.
Plants in foreground are controls held at 75° F.

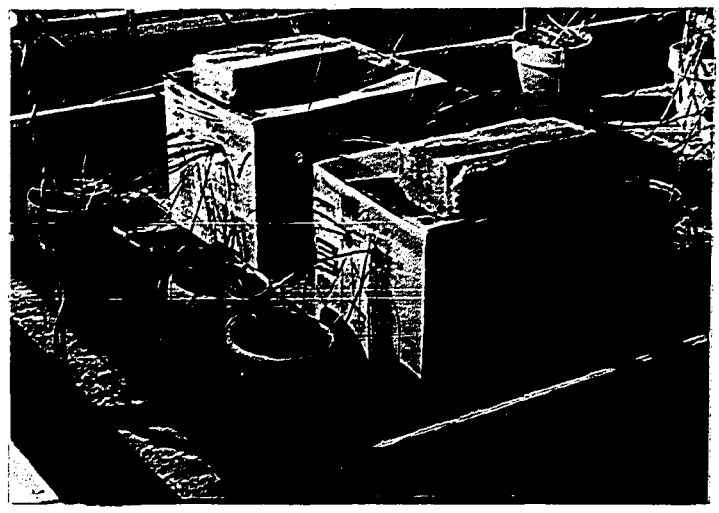


Figure 3. Method of testing effects of cool temperature on plant leaves. Air temperature was held at 45° F.
Boxes: (rear) heated to 60° to 65° F., (front) unheated control.
Plants surrounding boxes are controls.

box. The boxes were opened for short periods every 1 to 2 days only to water the plants and at other times to check the thermometers placed within.

Photoperiod Treatments

Two photoperiods of 11 and 18 hours were applied in both a warm and a cool greenhouse during the winter of 1955-56. A single bench in each greenhouse was divided by black, light-proof curtains which were hung on pipes and were opened each morning and closed each night. Although the short-day enclosures were open at the top, the light intensity readings within were less than 1 foot-candle at night. After February 24, however, the days in Ames gradually increase beyond 11 hours so that the 11-hour photoperiod could only be strictly maintained until this date. The photoperiods were controlled by Paragon time clocks and the supplemental illumination of approximately 100 foot-candles at the soil level was maintained by 200- and 300-watt bulbs spaced about 2.5 feet apart. To partially compensate for the longer period of illumination on 18-hour photoperiods, the plants on 11 hours received supplementary illumination all day.

In order to replicate photoperiods in Experiment 1, an additional pair of chambers were built in 1956. These were boxes 50 inches deep by 35 inches high by 39 inches wide placed side by side and equipped with two 15-watt fluorescent tubes and a 200-watt incandescent bulb each. The top

consisted of a cover which was removed during the day and closed at night. The chambers faced south and the front was closed by a black curtain during the night. Photoperiods of 11 and 18 hours were used.

In the photoperiod experiments of the 1956-57 season essentially the same facilities were used in the cool and the warm greenhouses with the exception of the two chambers described above which were discarded as unsatisfactory. However, three new additions were made. The cold frames described earlier were lighted with three 100-watt bulbs in each frame, with the 11- and 18-hour photoperiods being controlled by Paragon timers. The intensity of the supplemental illumination was 30 to 40 foot-candles at the plant level.

A space of about 6 feet along one bench in a warm greenhouse was also obtained for plants on 18-hour photoperiods. Again, 200-watt bulbs were used for supplementary illumination, which varied between 80 and 150 foot-candles intensity.

The third addition to the photoperiod facilities in 1956-57, as shown in Figure 4, was a series of ten light-proof compartments or cubicles constructed on a 30-foot greenhouse bench running east and west. These cubicles were 50 inches deep, 44 inches high and 35 inches wide, with the exception of an end chamber which was slightly wider. The partitions between each chamber consisted of frames constructed of wood 4 inches wide leaving the entire mid-portion open to enable

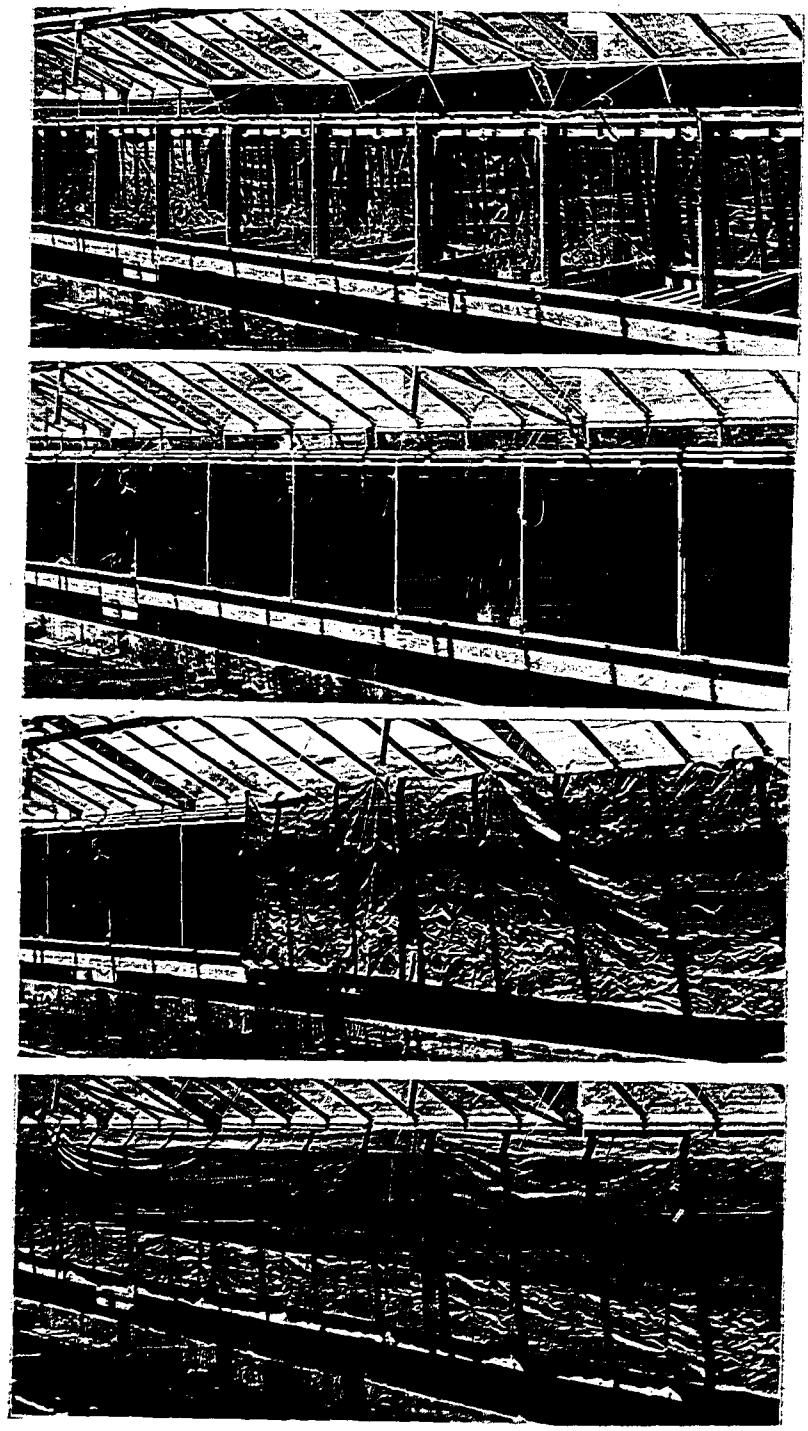


Figure 4. Photoperiod chambers used during 1956-57. Top to bottom: (a) chambers fully open during day, (b) covers down, shades drawn, (c) same, front curtain half drawn, (d) curtain fully drawn and fastened down, chambers fully closed for evening.

light passage during the day. Yellow, plastic-covered and light-proof window shades were mounted on these frames and were used to separate the photoperiod treatments. The backs (north sides) of the cubicles were covered with a light-proof canvas and five removable canvas covers were fitted on top. During the day the top covers were slid over and behind the bench and the shades were run up to obtain maximum natural illumination. At night, on the other hand, the shades were drawn between the compartments, the top covers were closed and then a canvas curtain was drawn over the south or front side and fastened in place. The supplementary illumination in eight of the cubicles consisted of four 40-watt white fluorescent tubes evenly spaced 8.5 inches apart in each cubicle. Four 30-watt white fluorescent tubes were used in each of the other two cubicles. In addition, there were four 50-watt incandescent bulbs spaced in a rectangle between the fluroescent tubes within each of the ten compartments. Each cubicle was also equipped with a separate time clock to regulate its own photoperiod. However, since the shortest photoperiod desired was 11 hours, one 11-hour clock controlled all of the fluorescent tubes of five adjacent compartments and an 11-hour clock at the other end controlled the fluorescent tubes in the other five compartments. The individual clocks controlled the incandescent lights in each cubicle. The fluorescent lights, therefore, were on from 6:30 a.m. until 5:30 p.m. daily, at

which time the 11-hour day ended and the curtains were closed. The supplemental incandescent illumination was timed so that, as nearly as possible, its duration was the same for all compartments. This involved having the incandescent lights on during the day for the shorter photoperiod treatments.

The intensity of the incandescent illumination ranged from about 40 foot-candles at one foot above pot level to about 90 foot-candles at one foot from the lights. Light of such low intensity is sufficient for a photoperiodic effect but lessens the possibility of growth differences among plants on different photoperiods. The 40-watt fluorescent illumination, however, was more intense, ranging from 120 foot-candles at a foot above pot level to perhaps a maximum of 800 to 900 foot-candles within a few inches of a tube. The intensity supplied by the 30-watt fluorescent tubes was about 30 to 40 foot-candles lower.

Chemical Treatments

A few experiments were carried out to study the effects of certain chemicals on the floral development of Minter wheat. The two compounds, α-naphthalene-acetic acid and the sodium salt of 2,3,5-triiodobenzoic acid were selected for use as an auxin and an anti-auxin and the more recently recognized gibberellic acid was also tested. All three compounds were applied to Minter plants as a foliage spray using

a modified DeVilbis atomizer. Tergetol 7[1] was added to all solutions at a concentration of 0.1 per cent by volume to act as a wetting agent. The sodium salt of triiodobenzoic acid was produced by titrating a given amount of the water-insoluble acid with sodium hydroxide to a pH of about 8.0.

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[1] A sodium heptadecyl sulfate.

EXPERIMENTAL RESULTS

In presenting the results of the 21 experiments following, an attempt was made to group experiments into (a) those conducted on the effects of cool temperature, (b) those conducted mainly on effects of photoperiod, and (c) those conducted on the effects of chemicals. The second group (b) also contains experiments involving photoperiod and temperature interactions. It should be understood that this grouping neglects chronological order and that it does not completely separate the effects studied in all experiments.

Temperature Effects

Several experiments were designed to study certain aspects of the floral response of Minter wheat to cool temperatures. Experiments 1 and 1A concerned seed vernalization while Experiments 2, 4, and 5 involved the effects of cool temperature on growing plants. All of these were conducted during the fall-winter-spring season of 1955-56. Experiment 14 was conducted during the 1956-57 season and involved vernalization in both seeds and plants.

Effects of duration and temperature of seed vernalization

Previous experiments with Pawnee and Minter wheat plants had indicated that the earliness response to increasing periods of cool temperature was more rapid after an initial lag phase of 2 to 4 weeks (2). It was also of interest to

determine the optimal vernalization times and effects of sustained vernalization in Minter wheat. Minter was selected because it had appeared to respond more readily to shorter periods of cool temperature than the Pawnee variety.

Experiment 1 The effects of temperature during seed vernalization and the length of vernalization treatment were investigated. The treatments consisted of two vernalization temperatures (1° C. and -2° C.) and eight durations of seed vernalization including the control or non-vernalized seed. After soaking the seeds in water and starting their germination, the excess water was drained off and the seeds were placed in 100 ml beakers within light-proof plastic containers at the desired temperature. In order to plant all of the seeds on the same date the vernalization of approximately 7 to 10 ml batches of seed was started at 8, 7, 6, 5, 4, 3, and 2 weeks prior to the time of planting on January 22, 1956. The controls were seeds soaked for about 24 hours prior to planting. The seeds were sown in 5-inch pots and uniformly thinned to two plants per pot a week after planting. A randomized block design was used with four replications of one pot per treatment per replication. The plants were maintained under 18-hour photoperiods for the entire period and the dates of awn emergence of the main tiller of each plant were recorded.

As shown in Table 2, freezing temperatures during vernalization of the seeds failed to cause any acceleration of heading. Some of the first and second foliage leaves of plants from seeds vernalized at -2° C. were noticeably injured and germination of the seeds was slow. The effect is illustrated in Figure 5. Hänsel's (39) results with winter rye indicate that temperatures as low as -4° C. can be effective in vernalization, however.

With respect to vernalization at 1° C., it is apparent that little or no acceleration of heading was obtained by vernalization times of less than 3 weeks. This effect is more easily observed in Figure 6. The analysis of variance of the 1° C. vernalized seeds, as shown in Table 3, revealed highly significant differences among the vernalization times and between the vernalized and the water-soaked, but unvernalized, treatments. After the initial lag phase, there was a rapid decrease in heading time with increase in time of vernalization. The differences in rates of development of plants from seeds vernalized for 5, 6, and 8 weeks are illustrated in Figure 7.

Experiment 1A After the planting of Experiment 1, some of the seeds remaining were returned to the refrigerator and held for longer periods of time. On May 6, 1956, seeds of this group were planted which had been vernalized for 9, 17, 18, or 19 weeks at 1° C. Water-soaked control seeds also were

Table 2. Effects of vernalization time and temperature on earliness of heading of Minter wheat on 18-hour days (Experiment 1)

Vernalization temperature	Vernalization duration (weeks)	Plants observed	Time from planting to awn emergence (days)
water-soaked controls		14	150
-2° C.	2	4	153
-2° C.	3	4	146
-2° C.	4	4	145
-2° C.	5	6	133
-2° C.	6	4	141
-2° C.	7	6	150
-2° C.	8	6	151
1° C.	2	6	140
1° C.	3	8	144
1° C.	4	8	121
1° C.	5	8	84
1° C.	6	8	59
1° C.	7	8	50
1° C.	8	8	43

Table 3. Analysis of variance of 1° C. data in Table 2

Source of variation	D.f.	M.s.	"F" ratio
Replications	3	126.333	
Treatments	7	8502.17	$21^{7}F=55.18^{**}$
Controls vs. vernalized	1	16848.03	$25^{1}F=120.73^{**}$
Among vernalized	6	7111.20	$21^{6}F=46.15^{**}$
Error	25	139.55	
Controls within replications	4	63.25	
Replications x vernalized	21	154.09	

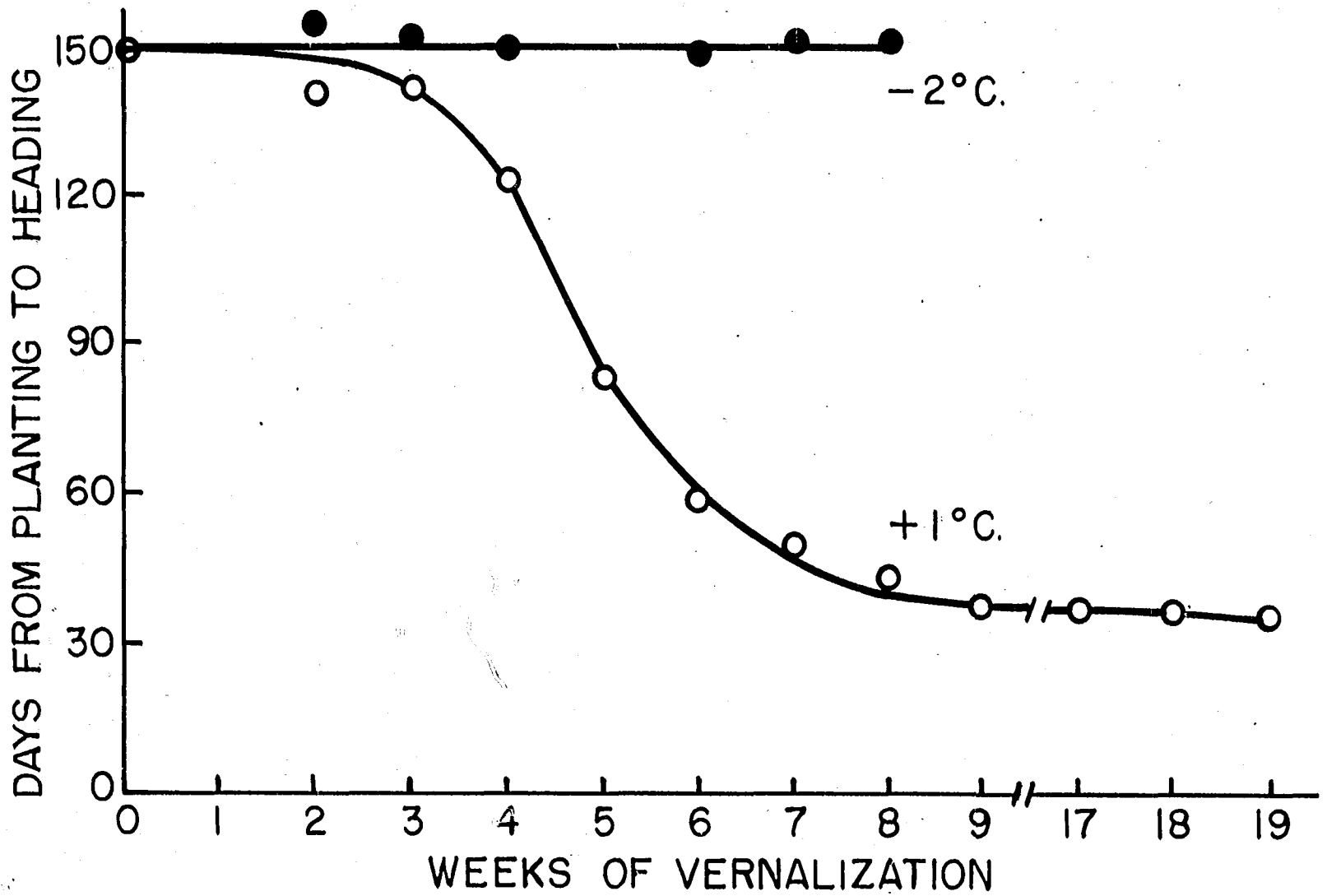
**Significant at 1 per cent level.

planted and the experiment was replicated four times. The plants were handled in the same manner as those in Experiment 1 and the dates of awn emergence and the number of leaves per plant at heading was obtained. Results of this experiment are shown in Table 4 and Figure 5.

From the data in Table 4 and the analysis of variance in Table 5 it is evident that there was a small but significant decrease in time to heading with seed vernalization beyond 9 weeks. Although the exact times from planting to heading may not be strictly comparable with those from Experiment 1 because the plants were grown at different times and the natural light intensities were somewhat different, the results

Figure 5. Effects of temperature after 8 weeks of seed vernalization.
(left) Plants from seeds vernalized at 1° C.
(right) Plants from seeds vernalized at -2° C.
Plants were 5 weeks old and grown at 75° F. and under 18-hour photoperiods.

Figure 6. Effects of vernalization times and two temperatures on earliness of heading of Minter wheat under 18-hour photoperiods and 75° F. temperatures.


DAYS FROM PLANTING TO HEADING
150
120
90
60
30
0
−2°C.
+1°C.
0
1
2
3
4
5
6
7
8
9
17
18
19
WEEKS OF VERNALIZATION

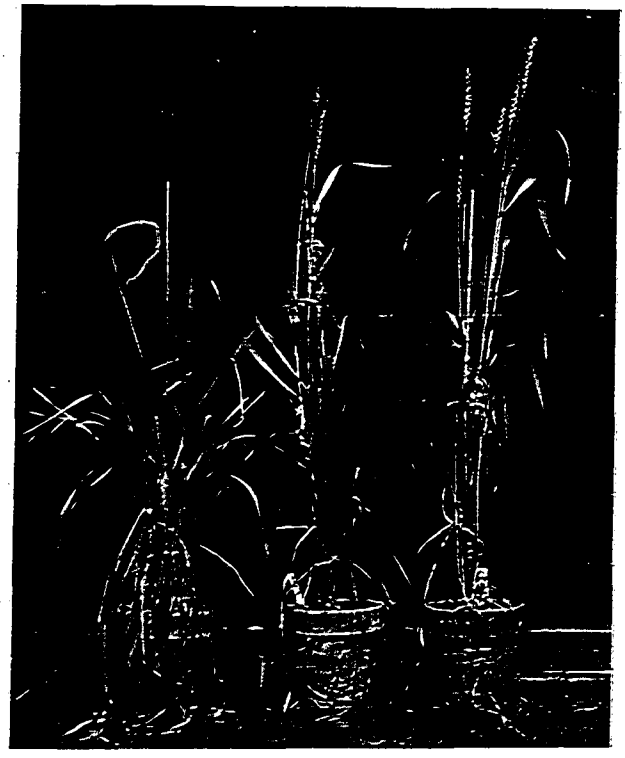


Figure 7. Effects of duration of seed vernalization at 1° C. on development of Minter wheat under 18-hour photoperiods.
Left to right: (a) 5 weeks, (b) 6 weeks, (c) 8 weeks.
Picture taken 63 days after planting.

Table 4. Earliness of heading and leaf numbers of long-time vernalized Minter wheat seeds on 18-hour days (Experiment 1A)[a]

Vernalization duration (weeks)	Plants observed	Time from planting to awn emergence (days)	Final leaf number
9	8	38	6.3
17	8	37	6.3
18	8	36	5.8
19	8	34	5.1

[a]Seeds vernalized at 1° C. after soaking.

Table 5. Analysis of variance of data in Table 4 (Time from planting to awn emergence)

Source of variation	D.f.	M.s.
Replications	3	0.1823
Vernalization times	3	8.5830**
Error	9	0.9740

**Significant at 1 per cent level.

also are included in Figure 5 to illustrate the effects of continued low temperatures. It will be noted that long periods of seed vernalization resulted in very rapid heading with as few as five leaves per plant being formed. Dissections of the vernalized seed at planting time revealed four leaf primordia already formed. These results correspond closely with those of Gott, Gregory and Purvis (32) who observed a minimum leaf number of five in Petkus winter rye. Earlier work with rye and wheat (59, 67) had indicated that seven was the minimum leaf number, but this was probably true only because seed vernalization had not been carried on long enough. Thus, from Experiments 1 and 1A, it can be concluded that increasing times of seed vernalization result in decreased times to heading and decreased leaf numbers to an apparent minimum of five leaves or only one leaf more than is found in the germinated seed. Purvis and Gregory (68) have suggested that the plant is fully thermo-induced or in a condition of "ripeness to flower" when the final leaf primordium appears, since after this only spikelet primordia are produced. It is at this point that the photoperiodic reactions are assumed to become important in affecting the initiation of spikelet primordia although the spikelets are not truly distinguishable until later.

Additive effects of cool temperature

With the knowledge obtained in previous experiments that

vernalization periods of 2 to 3 weeks duration were only slightly effective in causing acceleration of heading, it was of interest to determine whether the effects of such "suboptimal" cool-temperature treatments were additive. Experiments 2 and 14 were conducted partially for this purpose. The photoperiod effects also involved in Experiment 2 are covered in a later section. In both experiments, average weekly temperatures in the cool greenhouse were about 46° F. while the warm greenhouse temperatures averaged about 75° F. in Experiment 2 and 68° F. in Experiment 14. The seed vernalization techniques used in Experiment 14 are described in the MATERIALS AND METHODS.

Experiment 2 This experiment involved the exposure of plants to alternating 1- or 2-week periods of cool temperatures. Sixty 5-inch pots of Minter wheat were planted on November 25, 1955 and held at warm temperatures. The plants were thinned uniformly to two per pot and the pots were grouped into four replications of 15. The cool-temperature treatments were started 3 weeks after planting. The first eight treatments consisted of a 2x2x2 factorial with all combinations of two cool photoperiods of 11 and 18 hours, two warm photoperiods of 11 and 18 hours and two times of exposure to the alternating cool and warm temperatures, of 1 and 2 weeks. A total of 6 weeks of cool temperature was applied in all of these treatments but the lengths of the alternating

cool and warm temperatures differed so that four of the eight pots of each replication were on alternating 1 week cool, 1 week warm temperatures and the other four were on alternating 2 weeks cool, 2 weeks warm temperatures. After the total of 6 weeks of cool temperature was attained the plants were transferred for a final period to warm temperatures and 18-hour photoperiods. The alternating "1-week" plants returned to the warm temperatures a week later than the "2-week" plants. Table 6 outlines the treatments and summarizes the results of the heading data obtained, and an accompanying analysis of variance is given in Table 7.

The remaining seven treatments were included as controls. Two pots from each replication were transferred to the cool temperatures at the same time as the alternating temperature plants and remained there for a continuous 6-week period, four pots under 11 hours and four under 18 hours. After the 6 weeks of cool temperature they were returned to the warm greenhouse and placed under 18-hour photoperiods. Two other pairs of treatments consisted of plants transferred to the two cool photoperiods at 3 weeks and 7 weeks after planting. These plants were then returned to the warm greenhouse and to 18-hour photoperiods at the same time as the "2-week" plants. One set, therefore, received 6 weeks of cool temperature while the second set received 10 weeks of cool temperature.

The final treatment was the warm-long control consisting of the four pots which received no cool temperatures and were

Table 6. Effects of alternating temperatures and photoperiods on induction of Minter wheat as measured by earliness of heading on subsequent 18-hour days (Experiment 2)[a]

Induction treatment[b]	Time from planting to heading (days)	Time from end of last cool temp. to heading (days)	Time from end of last cool temp. to heading avgs. (days)
(1) CL-1 wk→WL-1 wk 6 cycles	139	41	38.5
(2) CL-1 wk→WS-1 wk 6 cycles	134	36	
(3) CL-2 wk→WL-2 wk 3 cycles	138	47	46.0
(4) CL-2 wk→WS-2 wk 3 cycles	136	45	
(5) CS-1 wk→WL-1 wk 6 cycles	140	42	39.5
(6) CS-1 wk→WS-1 wk 6 cycles	135	37	
(7) CS-2 wk→WL-2 wk 3 cycles	138	47	47.0
(8) CS-2 wk→WS-2 wk 3 cycles	138	47	
(9) WL-3 wk→CL-6 wk	99	36	36.0
(10) WL-3 wk→CS-6 wk	99	36	
(11) WL-7 wk→CL-6 wk	127	36	36.0
(12) WL-7 wk→CS-6 wk	127	36	
(13) WL-3 wk→CL-10 wk	119	28	29.0
(14) WL-3 wk→CS-10 wk	121	30	
(15) WL controls	150	-	

[a] All but last 3 treatments received a total of 6 wks. of cool temperatures (45° F. avg.); there were 8 observations per treatment.

[b] CS=cool-short WS=warm-short
CL=cool-long WL=warm-long

Table 7. Analysis of variance of data in Table 6 (Days from end of cool temperature to awn emergence)[a]

Source of variation	D.f.	M.s.	"F" ratio
Replications (R)	3	9.61	
"Alternating" treatments (A)	7	85.14	$_{20}^{7}F=5.80^{**}$
Times (T)	1	457.53	$_{20}^{1}F=31.19^{**}$
Cool photoperiods (CP)	1	16.53	$_{20}^{1}F=1.13$ N.S.
CP x T	1	0.03	$_{20}^{1}F=0.002$ N.S.
Warm photoperiods (WP)	1	75.03	$_{20}^{1}F=5.11^{*}$
WP x T	1	42.78	$_{20}^{1}F=2.92$ N.S.
WP x CP	1	1.53	$_{20}^{1}F=0.104$ N.S.
WP x T x CP	1	2.55	$_{20}^{1}F=0.173$ N.S.
Continuous cool-temperature treatments (CT)	5	56.79	$_{15}^{5}F=27.29^{**}$
CT vs. A	1	1123.75	$_{3}^{1}F=102.07^{**}$
Error	38[b]	9.41	
A x R	20	14.67	
CT x R	15	2.08	
(CT vs. A) x R	3	11.01	
Cool-long 10 weeks vs. cool-short 10 weeks	1	98.0	$_{15}^{1}F=47.09^{**}$

[a]Excluding warm-long controls.
[b]One missing value reduced Error degrees of freedom by one.
*Significant at 5 per cent level.
**Significant at 1 per cent level.
N.S. Not significant at 5 per cent level.

held under 18-hour photoperiods until heading. The data obtained were the times from planting to awn emergence and the times from the end of the last cool-temperature treatment to awn emergence.

The data in Table 6 (treatments 9 to 15) on the days from planting to heading indicate that the earlier the cool-temperature treatments were completed the shorter the time from planting to heading. This is pointed out by the fact that plants receiving 6 weeks of cool temperature starting at 7 weeks after planting headed exactly 4 weeks later than plants receiving the same cool-temperature treatment but starting 4 weeks earlier. Thus, as has been noted in previous experiments, cool temperature appears to delay initiation and further development while favoring induction. Therefore, it is more reasonable to compare the times from the end of the cool-temperature period to heading in evaluating the effects of cool-temperature treatments applied at different times.

To properly evaluate the additive effects of the alternating cool-temperature treatments, additional control treatments should have been included in the experiment. However, in Table 6, it is seen that the warm-long controls headed later than the cyclic treatments and, therefore, there was some effect of the short periods of cool temperature in accelerating heading. The comparisons among days from the last cool temperature to heading point out significant differences

among the "alternating" treatments which are given also in Table 7. Six 1-week periods of cool temperature were somewhat more effective than three 2-week periods (treatments 1, 2, 5, and 6 vs. 3, 4, 7, and 8). The explanation for the apparent promotive effects of the six 1-week treatments is that the intermittent periods of 1 week of warm temperature were not long enough to cause a great loss of the vernalization response, whereas the 2-week periods of warm temperature probably were. Partial devernalization during the 2-week periods of warm temperature is suggested.

The data in Table 6 show that some of the six "1-week" treatments were as effective in promoting earliness as were the continuous "6-week" treatments (treatments 2 and 6 vs. treatments 9 to 12). From this data it was concluded, therefore, that the effects of suboptimal periods of cool temperature were at least partially additive but these effects were less additive as the intermittent period of warm temperature increased from 1 to 2 weeks.

Although not related to the additive effects of cool temperature, treatments 9 through 12 in Table 6 point out the lack of effect of previous plant growth on the response to 6 weeks of cool temperature. Plants treated with cool temperature either at 3 or 7 weeks of age all headed 36 days after the cool-temperature period. It would be expected that the 7-week plants would have progressed somewhat in floral induction and, therefore, that these plants should have headed

earlier after the cool temperature. This is in accordance with the ideas of Purvis and Gregory (68) who have postulated an autocatalytic production of the flower-inducing state at warm temperatures.

That the 7-week plants (treatments 11 and 12) headed at the same time as the 3-week plants (treatments 9 and 10), therefore, suggests that the inductive effect of 3 to 7 weeks of growth is rather negligible compared to inductive effects of the cool-temperature treatment. Further evidence is presented on this subject in Experiment 2 and also in Experiment 17 which follows in a later section.

Experiment 14 This experiment differed from Experiment 2 in that the cool temperatures were applied to partially germinated seeds as well as to growing plants. The 18 induction treatments were arranged in a randomized block design and replicated four times. The first eight treatments were a three-factor factorial with two seed vernalization times of 0 and 3 weeks, two periods of warm temperature after planting of 1 and 4 weeks, and two subsequent periods of cool temperature in the greenhouse of 2 and 4 weeks.

In addition to the above eight, ten treatments also were included as controls or added comparisons. Four of these treatments consisted of seeds vernalized for 2, 3, 5, and 14 weeks, with no subsequent cool temperatures after planting and five others consisted of 2, 3, 5, 6, and 8 weeks of cool

temperature applied to the seedlings immediately after sowing the unvernalizaed seeds. The final treatment was a group of plants held at warm temperatures continuously.

The seed vernalization treatments were started prior to planting so that all treatments were planted on December 30, 1956. The standard photoperiod conditions during the plant induction treatments were 11 hours at the cool temperature and 18 hours at the warm temperatures. After the completion of the induction treatments, the plants were held under 18-hour photoperiods and warm temperatures until heading.

The data on the times from planting to heading and for the end of the cool temperature treatments to heading are summarized in Table 8. The analysis of variance of the times from planting to heading is given in Table 9. The times from planting to heading are largely used in evaluating treatment comparisons for plants which completed their cool temperatures at the same time, while the data on times from the end of the cool temperature to heading are used in evaluating treatment comparisons for plants which completed their cool temperatures at different times. The reasons for this have been discussed in Experiment 2 but are based upon the assumption that the cool temperatures used in these experiments promote floral induction but delay floral initiation.

The comparisons of main interest in Table 8 are those among the factorial treatments and the various controls.

Table 8. Additive effects of seed vernalization and plant vernalization on earliness of heading of Minter wheat (Experiment 14)

	Induction treatments			Heading data	
	Seed vernalization[a] (weeks)	Warm temp. (weeks)	Plant vernalization[b] (weeks)	Time from planting to awn emergence (days)	Time from end of cool temperature to awn emergence (days)
(1)	3	1	2	95	74
(2)	3	1	4	86	51
(3)	3	4	2	117	75
(4)	3	4	4	105	49
(5)	0	1	2	135	114
(6)	0	1	4	99	64
(7)	0	4	2	128	86
(8)	0	4	4	106	50
(9)	2	0	0	126	126
(10)	3	0	0	113	113
(11)	5	0	0	64	64
(12)	14	0	0	50	50
(13)	0	0	2	139	125
(14)	0	0	3	122	101
(15)	0	0	5	87	52
(16)	0	0	6	87	45
(17)	0	0	8	96	40
(18)	0	continuous	0	136	-

[a]Seed vernalization at 1° C.

[b]Cool greenhouse average weekly temperatures ranged from 41° to 49° F.

Table 9. Analysis of variance of data in Table 8 (Time from planting to awn emergence)

Source of variation	D.f.	M.s.	"F" ratio
Replications (R)	3	73.29	
Factorial treatments (F)	7	1144.55	$_{20}^{7}F$=35.05**
Vernalization times (V)	1	2202.83	$_{20}^{1}F$=61.63**
Warm temperature times (W)	1	825.20	$_{20}^{1}F$=23.09**
Cool temperature times (C)	1	3230.08	$_{20}^{1}F$=90.38**
V x W	1	815.06	$_{20}^{1}F$=22.81**
V x C	1	717.20	$_{20}^{1}F$=20.06**
C x W	1	70.50	$_{20}^{1}F$=1.97 N.S.
C x V x W	1	151.00	$_{20}^{1}F$=4.22 N.S.
Other treatments (O)	9	3195.17	$_{27}^{9}F$=51.36**
Others vs. Factorial	1	178.86	$_{3}^{1}F$=3.54 N.S.
Error	50	50.92	
F x R	20	35.74	
O x R	27	62.21	
(O vs. F) x R	3	50.46	

**Significant at 1 per cent level.

N.S. Not significant at 5 per cent level.

Considering the times from planting to heading, the 2-week periods of cool temperatures applied either to the seeds or growing plants resulted in little acceleration of heading as compared with the warm temperature controls (treatments 5, 7, 9, and 13 vs. 18). However, 3 weeks of seed vernalization were significantly more effective than no seed vernalization in almost all of the factorial treatments (treatments 1 to 3 vs. 5 to 7). The exception was the separation of 3 weeks of seed vernalization and 4 weeks of plant vernalization by a 4-week period of warm temperatures (treatment 4 vs. 8). In this case the promotive effects of the 3 weeks of seed vernalization appeared to have been lost during the long period of warm temperatures following, for the plants headed no earlier than those receiving only the 4 weeks of plant vernalization. This "apparent" devernalization did not occur where the final cool-temperature treatment was 2 weeks (treatment 3 vs. 7). Therefore, it is probable that the "apparent" devernalization was rather a result of interaction of seed vernalization and plant age at the time of the last cool-temperature treatment than of a complete loss of the effect of 3 weeks of seed vernalization.

There is evidence for this conclusion from two observations in Table 8. In comparing the times from the end of the cool-temperature treatments to heading in treatments 1 and 3, it is seen that the same response was obtained regardless of the intermediate warm temperature period. That is, 1 week or

4 weeks of warm temperatures between 3 weeks of seed vernalization and 2 weeks of plant vernalization both resulted in heading at about 75 days after final removal from the cool temperatures. However, with plants receiving no seed vernalization (treatments 6 and 8) the promotive effect of the 4 weeks of warm temperatures over the effect of 1 week of warm temperatures was 14 days, which is considered significant. The interaction of seed vernalization with warm-temperature treatment also is shown to be significant in the analysis of variance in Table 9. Therefore, it is concluded that the effects of seed and plant vernalization were at least partially additive but that in the absence of a seed vernalization treatment plant growth was important in determining the response to cool temperature.

In Experiment 2 evidence was presented which indicates that this promotive effect of plant growth preceding cool temperature treatment reaches a maximum when the plants are 3 weeks of age. Plants of this age usually have three to four visible leaves, several microscopic leaves and several tillers or tiller buds, when grown under warm temperatures. The possibility exists that the promotive effects of plant growth during these first few weeks after planting are due to the increased numbers of tiller buds which increases the number of loci receiving the cool temperature effect. Another possible explanation is that there is an autocatalytic production of the induced state under warm temperatures which is added to

the cool temperature induction product. This explanation would be in keeping with the theories of Purvis and Gregory (68) on flowering of the winter cereals.

That the effects of the seed and plant vernalization treatments were not completely additive also is shown in Table 8. Three weeks of seed vernalization followed by 2 weeks of plant vernalization resulted in heading 74 to 75 days after treatment while 5 continuous weeks of plant vernalization caused heading to occur 52 days after treatment (treatments 1 and 3 vs. 15). Five weeks of seed vernalization caused heading to occur in 64 days (treatment 11) which was still less than with the split treatment. On the other hand, a total of 7 weeks of combined seed and plant vernalization caused heading to occur in about the same time as in plants receiving 5 continuous weeks of plant vernalization (treatments 2 and 4 vs. 15).

Receptor of the cool temperature response

Although it has been assumed that the apical meristem is the receptor of the cool temperature stimulus in the winter annuals, it was of interest to determine whether the leaves of wheat could also act as receptors. A small experiment was conducted in which the leaves of Minter wheat were exposed to cool temperatures while the growing points were held at warm temperatures.

Experiment 4 Eighteen 4-inch pots of Minter wheat were sown on January 3, 1956 and thinned to two uniform plants. After 2 weeks at warm temperatures, 12 of the pots were transferred to the cool greenhouse and 11-hour photoperiods. Four pots were placed in the corners of each of two cardboard boxes and holes were pierced in the boxes, each hole being placed so as to allow a single plant to grow through it. The leaves were then guided through the holes and cotton was used to fill the gaps. In one box a 25-watt light bulb was placed in the middle and covered with aluminum foil to exclude light. The top covers of both boxes were closed, allowing only a small amount of light into the boxes during the 11-hour day. Four pots also were held on the bench beside the boxes. Temperature readings taken with thermometer located in the heated box varied between 60° and 80° F., but were always above 60° F. The temperatures in the unheated box were a few degrees higher than the greenhouse temperature in bright sunlight but dropped to room temperature at night. The average weekly temperatures in the room ranged between 40° and 46° F. for the 6 weeks that the plants remained in the boxes.

At the end of the 6-week period two plants were harvested and dissected from each of the four positions and observations were made on leaf numbers, numbers of tillers, and floral development. The rest of the plants were returned to the warm greenhouse and held under 18-hour photoperiods.

As shown in Table 10 the plants in the heated box produced more tillers and leaves than the plants in the unheated box or in the open cool greenhouse but slightly fewer leaves than the warm temperature controls. All plants observed were vegetative at this date.

Table 10. Effects of cooling the leaves of Minter wheat for 6 weeks at 45° F. on floral initiation and earliness of heading (Experiment 4)

Treatment	After 6 weeks at cool temperatures			After 8 more wks. at 75° F. and 18-hr. photoperiods	
	Total no. of leaves	Floral state	Number of tillers	Stage of development[a]	Plants observed
Warm temp. controls	16.4	veg.	2.3	3.2	6
Heated box[b]	14.5	veg.	5.5	1.7	6
Unheated box	11.0	veg.	2.0	5.5	6
Cool temp. controls (no box)	10.5	veg.	2.0	5.4	10

[a]Stages of development based on arbitrary scale.
1 = vegetative
2 = beginning of double ridge formation
3 = 3 or more double ridges
4 = ridges fused, smooth primordia
5 = preheading stages, lemmas, stamens, awns all present
6 = heading

[b]Leaves were exposed to 45° F. and culms to 65° F. temperatures.

The plants transferred to warm temperatures and 18-hour photoperiods were dissected after 8 weeks under these conditions and the data on the stages of spikelet development also are shown in Table 10. The system for rating the stages of development in this experiment differed from the later system used in that the range was from 1 to 6, whereas the later system included stages ranging from 1 to 10. The plants formerly held in the heated box were still vegetative while even the warm temperature controls were beginning to initiate spikelet primordia. In contrast, the plants previously held outside the boxes were distinctly advanced in their spikelet development.

The analysis of variance of the data on stages of development of the growing points is shown in Table 11. Differences

Table 11. Analysis of variance of data on stages of development in Table 10

Source of variation	D.f.	M.s.
Treatments	3	11.2566**
Error	11	0.2421

**Significant at 1 per cent level.

among induction treatments are significant at the 1 per cent level. Thus, although most of the leaf area of the plants in the heated box actually received cool temperatures, the vernalization process was inhibited by the high temperatures surrounding the culms and roots. Since the roots also were heated, it cannot be concluded from this experiment that the apical meristem itself is the receptor of the cool temperature stimulus. However, this is thought to be the case.

Devernalization by heat

Work of Gregory and Purvis (36) and others (44) indicated that vernalization of seeds of rye and wheat could be reversed by subsequent high-temperature treatment. In Experiment 5 the effects of high temperatures on vernalized plants were determined.

Experiment 5 The high-temperature treatment was carried out by placing vernalized plants inside transparent plastic chambers. Seeds of Minter wheat were sown in 12 4-inch pots on December 5, 1955 and the seedlings were thinned to two uniform plants. The plants were then transferred to the cool temperature greenhouse. After 6 weeks at the cool temperatures the plants were transferred to the greenhouse and four pots were placed in each of the two transparent chambers. The frames as shown in Figure 2 were covered with a transparent polyethylene plastic. One of the chambers was heated to about $95^{\circ} \pm 5^{\circ}$ F. by placing a 25-watt light bulb under an

overturned pot. The other chamber was warmer than the air temperature or about 85° ± 5° F., while the temperatures on the bench outside the chambers were about 75° ± 10° F. Temperatures in all three positions fluctuated somewhat during sunny days.

After 3 weeks the plants were removed from the chambers and the two plants from one pot of each of the three positions (heated and unheated chambers and controls) were dissected and the number of leaves and the floral condition of the spike were observed. The rest of the plants, a total of six from each treatment, were allowed to head under the 18-hour photoperiods and the dates of awn emergence were recorded. The data are shown in Tables 12 and 13.

After 3 weeks in the chambers, the plants from the heated chamber had developed two fewer leaves but were slightly more advanced in initiation of spikelet primordia than the controls and plants from the unheated chambers. The plants which headed all emerged from the sheath about the same time, indicating no devernalization effects by the high temperatures. It will be remembered that the plants received a period of cool temperatures which normally causes rapid heading under subsequent warm temperatures and long photoperiods. Other workers (44, 69) have reported that devernalization by heat decreases as the time of vernalization increases. Observations in Experiment 2 tend to support this explanation even though normal greenhouse temperatures were used.

Table 12. Effects of high temperatures immediately after vernalization of Minter wheat plants on floral initiation and earliness of heading (Experiment 5)

Treatment	After 3 weeks in transparent plastic boxes		Heading data on plants removed from boxes	
	Total leaves	Flowering condition of spike	Plants observed	Time from planting to awn emergence (days)
Control (no chamber)	13	vegetative elongated	6	91
Heated chamber	11	double ridges almost visible	6	92
Unheated chamber	13	vegetative elongated	6	93

Table 13. Analysis of variance of data in Table 12 (Time from planting to awn emergence)

Source of variation	D.f.	M.s.
Treatments	2	3.083N.S.
Error	5	2.667
Total	7	

N.S. Not significant at 5 per cent level.

Photoperiod Effects

The effects of photoperiod on the floral development of winter wheat were studied in about 12 separate experiments. It was desired to determine the effects of photoperiod during every major phase of winter wheat development, including the cool temperature reactions.

In many of the experiments only two photoperiods of 11 and 18 hours were used. Eleven hours represents a fairly short day and can be maintained in Ames under natural illumination for a period of 3 to 4 months during the winter, whereas 18 hours represents a distinctly long day. In other experiments intermediate photoperiods or continuous light were used but in every case where the effects of different photoperiods were compared, attempts were made to compensate for the supplemental illumination supplied at night to the plants on long photoperiods by supplying the shorter-day plants with supplemental illumination during the day.

The results of the photoperiod experiments are presented in a developmental outline starting with the early phases of induction and leading to initiation and further development. Since cool temperature plays such an important role in flowering of winter wheat the experiments were placed into three groups according to the time of photoperiod application with respect to the cool temperature.

Photoperiod effects without cool temperatures

Previous research by several workers (42, 59, 67) had indicated that under continued warm temperatures winter wheat and winter rye flowered earliest under short photoperiods during early growth and long photoperiods following. Experiments 8 and 8A were designed to determine the magnitude of the promotion of flowering by short induction photoperiods. The variety Minter was used as in all other experiments. In addition, two older varieties, Harvest Queen and Turkey, also were tested because of the availability of literature on their past responses.

Experiment 8 The basic plan involved the exposure of Minter and Turkey seedlings to four different induction photoperiods for 6 weeks. In the split plot design with induction photoperiods as whole plots and the two varieties as the subplot treatments, each replication contained duplicate pots for each photoperiod-variety combination or a total of 16 5-inch pots of two plants each. Because of the lack of space in the photoperiod chambers, replications 1 and 2 were planted with unvernalized seeds on October 15, 1956 and replications 3 and 4 were planted 3 weeks later. After all the plants had been exposed to the 11-, 13-, 15.5-, or 18-hour photoperiods for 6 weeks at about 80° F., they were transferred to 18-hour photoperiods and 68° F. temperatures in

another greenhouse. The third replication later was placed under continuous illumination following a time-clock failure.

The original plan called for harvesting one of the duplicate pots per treatment at uniform times after removal from the photoperiod chambers. Because of the different planting times, replications 1 and 2 were harvested first at 23 days after the photoperiod treatments or at 10 weeks after planting. The numbers of tillers, the stages of development of the apex and the spike lengths were observed. At this time all the plants were vegetative and the spike lengths averaged about 0.5 mm for all treatments. As shown in Table 14,

Table 14. Effects of 6 weeks of four different photoperiods on the production of tillers in unvernalized Turkey and Minter wheats (Experiment 9)[a]

Variety	Induction photoperiod	Plants observed	Number of tillers per plant
Minter	11	8	6.6
	13	8	3.6
	15.5	8	4.4
	18	8	3.8
Turkey	11	8	7.0
	13	8	4.0
	15.5	8	4.5
	18	8	3.8

[a]Plants grown on 18 hours at 68° F. after treatment and harvested after 3 weeks.

however, the number of tillers per plant was much greater after 11-hour induction photoperiods than after any of the other three photoperiods.

Since no differences in floral development were observed in the harvested plants of replications 1 and 2, it was then decided to wait until a later date to harvest the remaining plants. The remaining plants from replications 1 and 2 were harvested on February 2, 1957, or 51 days after the end of the photoperiod treatments and 100 days from planting. The plants then were dissected and records were made of the spike lengths, the numbers of spikelet primordia and the stages of development of the apex. The means are shown in Table 15. The system by which these stages are used has been described completely in the MATERIALS AND METHODS and is illustrated in Figure 1.

The results of all three measurements show that the plants previously treated under 15.5-hour photoperiods were more advanced in their floral development. This apparent promotion by the 15.5-hour induction photoperiods is rather difficult to account for in the absence of a similar effect by the 18-hour treatment. If a 15.5-hour treatment promoted initiation, an 18-hour photoperiod should cause even greater promotion, for they are both distinctly long days. Therefore, this effect was not accepted as being meaningful.

Table 15. Effects of 6 weeks of three different photoperiods on floral development in unvernalized Turkey and Minter wheats on subsequent 18-hour days (Experiment 8)[a]

Variety	Induction photoperiod (hours)	Measurements obtained 51 days after end of induction treatment[b]		
		Stage of development	Number of spikelet primordia	Spike length (mm)
Minter	11	3.0	7.8	0.89
	13	2.3	4.3	0.87
	15.5	3.0	10.0	1.16
	18	3.0	8.5	0.86
Turkey	11	3.0	7.3	0.87
	13	3.0	7.3	0.83
	15.5	3.5	15.8	1.28
	18	3.0	8.5	0.93

[a]Each figure is an average of two replicates or four plants.

[b]68° F. temperatures.

Table 16 summarizes the results of the data from the replications 3 and 4 which were allowed to head under long photoperiods. The differences among induction photoperiods were variable and not significant as shown in Table 17. On the average Turkey headed earlier than Minter, especially after the longer induction photoperiods. With data of this type, few conclusions can be drawn from Experiment 8 except that any promotive effects of short photoperiods were rather small or non-existent during the 6-week periods of photoinduction.

Table 16. Effects of four induction photoperiods for 6 weeks on the heading of unvernalized Turkey and Minter wheat under subsequent 18- to 24-hour photoperiods (Experiment 8)[a]

Variety	Induction photoperiod	Days from planting to heading
Minter	11	143
	13	149
	15.5	154
	18	144
Turkey	11	146
	13	133
	15.5	140
	18	129

[a]68° to 80° F. temperatures.

Table 17. Analysis of variance of data in Table 16

Source of variation	D.f.	M.s.
Replications	1	689.04
Photoperiods	3	84.55 N.S.
Error (a)	3	71.75
Varieties	1	451.54**
Varieties x photoperiods	3	77.25
Error (b)	4	13.33

**Significant at the 1 per cent level.

N.S. Not significant at the 5 per cent level.

Experiment 8A As a supplement to Experiment 8, twelve 6-inch pots of unvernalized Harvest Queen wheat were planted on January 31, 1957 and distributed among six compartments of three different photoperiods (11, 14, and 18 hours). The 14-hour photoperiod was chosen in this case because it was intermediate between 11 and 18 hours. The plants were thinned to two per pot and held under these photoperiods and 80° F. temperatures for 11 weeks. They were then transferred to continuous light for 5 more weeks. At this time the main tillers were harvested and dissected and measurements were made of the spike lengths, numbers of spikelet primordia and the stages of floral development. From the data in Table 18 a promotive effect of the 11-hour induction photoperiods is evident. The average values for all three measurements support this conclusion, but the analysis of variance of the stage of development data in Table 19 shows no significant differences among the induction treatments. The low value for the spike lengths of the 14-hour treatment in Table 18 indicates the type of variability involved in that measurement, but it must be remembered that after initiation on long photoperiods the increase in spike length is exponential with time and large differences may occur as a result of only a few days delay. Results obtained by McKinney and Sando (59) with Harvest Queen winter wheat indicated a greater promotive effect of short photoperiods applied during early growth than was obtained in this experiment. These workers obtained.

Table 18. Effects of 11 weeks of three different photoperiods on floral development in unvernalized Harvest Queen winter wheat under subsequent continuous light (Experiment 8A)[a]

Induction photoperiod (hours)	Plants observed	Measurements obtained 35 days after end of induction treatment		
		Spike length (mm)	Number of spikelet primordia	Stage of development
11	8	20.99	22.1	7.6
14	6	2.01	19.3	4.7
18	10	13.36	20.6	6.6

[a]68° F. temperatures.

Table 19. Analysis of variance of data in Table 18. (Stage of development)

Source of variation	D.f.	M.s.
Photoperiods	2	5.058 N.S.
Error	9	1.895

N.S. Not significant at 5 per cent level.

greater effects using an 8-hour short day also, but their results with 12- to 14-hour days indicated that these day-lengths were considerably more effective in inducing unvernalized Harvest Queen than 17- and 18-hour days. Results from Experiment 8 showed no detectable responses of Minter and Turkey wheats to 6 weeks of 11-hour photoperiods and Experiment 8A was able to detect only a small response of Harvest Queen wheat to 11-hour photoperiods during an 11-week period. It is possible that the 6-week period was too short and the 11-week period too long for maximum promotive effect of the short photoperiods, for other workers have shown that the short photoperiods promote induction but delay initiation and further development (59, 67).

Photoperiod effects prior to and during cool temperatures

A total of four experiments were involved with the effects of photoperiods applied before and during cool temperature treatment. The general objective of these experiments was to determine the effects of photoperiod on the floral induction reactions in winter wheat.

The photoperiod conditions in Experiments 2, 3, and 17 were 11 and 18 hours and these were maintained by the use of dark curtains. In Experiment 10, however, 13-, 14-, and 18-hour photoperiods were imposed following cool-temperature treatments and these were maintained in the special photoperiod compartments described in the MATERIALS AND METHODS.

The 11- and 18-hour photoperiods were selected as examples of distinctly short and long photoperiods. In Experiment 11, the 13--and 14-hour photoperiods were selected because it was desired to obtain interaction of cool and warm photoperiods without undue delay in heading. The average weekly temperatures in the cool greenhouse ranged from 40° to 46° F. for Experiments 2 and 3 and from 40° to 58° F. for Experiments 10 and 17. The warm greenhouse temperatures averaged about 75° F. for Experiments 2 and 3 and about 68° F. for Experiments 10 and 17.

Experiment 2 One of the objectives of Experiment 2 was to determine the relative effects of long and short photoperiods applied during alternating cycles of cool and warm temperatures. The experiment is described in detail in the earlier section, Additive effects of cool temperature, and the outline of the treatments is given in Table 6. The eight main treatments involved a 2x2x2 factorial with two cool photoperiods of 11 and 18 hours, two warm photoperiods of 11 and 18 hours, and two periods of alternating temperature-photoperiod combination of 1 and 2 weeks. A total of 6 weeks of cool temperature was applied to the plants in this group, either in six 1-week or three 2-week periods. Seven additional treatments included the continuous warm temperature controls and three other pairs of treatments, two of which received 6 or 10 weeks of cool temperature starting at 3

weeks of age and one pair which received 6 weeks of cool temperature when the plants were 7 weeks of age. Each member of the treatment pairs was placed under one of the two cool photoperiods. Following the cool temperature applications all 15 treatments were transferred to 18-hour photoperiods at the warm temperatures and allowed to head. The results are summarized in Table 6 and an analysis of variance of the data on days from end of the cool temperatures to awn emergence is given in Table 7.

From Table 6 it is evident that cool photoperiods had no effect on earliness of heading under subsequent warm temperatures. This was true for all comparisons except treatments 13 and 14. Where 10 weeks of cool temperature were applied, cool-long photoperiods significantly accelerated heading by two days as compared with cool-short photoperiods. This promotive effect of long days during very long periods of cool temperature also has been found in Experiment 10, the results of which are yet to be presented.

Although photoperiods during cool temperatures of 6 weeks duration did not affect the earliness of heading, there was a significant effect of photoperiod during the intermittent warm temperatures in the "alternating" treatments. Short photoperiods during the 1-week periods of warm temperatures caused heading to occur 5 days earlier, on the average, than comparable 18-hour photoperiods. Thus it appears that a combination of alternating 1-week periods of cool and warm

temperatures and short photoperiods at the warm temperatures produced the earliest heading after the cool-temperature treatments. This is an interaction that, at present, is difficult to explain. However, it is significant, in light of other results obtained, that short photoperiods promoted induction during warm temperatures prior to the completion of the cool-temperature treatments. It is suggestive of a separation of the vernalization reactions and the photoperiodic induction reactions similar to the scheme proposed by Purvis and Gregory (68).

Experiment 3 This test was conducted during the 1955-56 season to determine the effects of photoperiod during and after the cool-temperature treatment of Minter wheat.

Fifty-four pots of Minter wheat were planted on November 25, 1955 and the resultant plants after thinning were held at warm temperatures for 3 weeks. All but six pots then were transferred to the cool greenhouse. Half of these pots were placed under each of the two cool photoperiods (11 or 18 hours). The six pots remaining in the warm greenhouse were equally distributed to the two photoperiod compartments. After 6 weeks at the cool temperatures the 48 other pots were returned to the warm greenhouse and six treatments were imposed on the 24 pots from each cool photoperiod. These treatments were as follows: (1) and (2) 2 weeks under 11 or 18 hours and then transfer to the opposite photoperiod, (3) and

(4) 4 weeks under 11 or 18 hours and then transfer to the opposite photoperiod, (5) and (6) 11 or 18 hours continuously. Treatments 5 and 6 were replicated six times and all the others were replicated three times. The treatments were grouped into three blocks under each of the photoperiods. Two complete replications were held in the curtained area in the greenhouse while the blocks of the third replication were placed in two special photoperiod compartments. Unfortunately these compartments proved unsatisfactory, probably because of poor light intensity and high temperatures, and the entire third replication was discarded.

The heading data are given in Table 20. Again it is evident that where the vernalized plants headed under long photoperiods at warm temperatures, the cool photoperiod had no effect on earliness of heading. However, where the vernalized plants were allowed to complete their development under short days, the plants which had been under short photoperiods at the cool temperatures headed from 6 to 9 days earlier than those previously under cool-long photoperiods. Therefore, short photoperiods at the cool temperatures appeared to accelerate heading only under the relatively inhibitory warm-short photoperiods. Variability of heading time increased with the delay in heading caused by the short photoperiods so that the apparent difference in this case may not be significant. An analysis of variance was not valid in this experiment since the photoperiod compartments were not replicated.

Table 20. Effects of photoperiod on earliness of heading of Minter wheat when applied during and after 6 weeks of cool temperature induction (Experiment 3)

Cool-induction photoperiod (hours)	Initial warm photoperiod and duration (hrs.)	(wks.)	Final warm photoperiod (hours)	Time from end of vernalization to awn emergence (days)	No. of reps.
11	11	-[a]	11	109	4
18	11	-[a]	11	118	4
11	18	2	11	74	2
18	18	2	11	81	2
11	18	4	11	38	2
18	18	4	11	44	2
11	18	-[a]	18	37	4
18	18	-[a]	18	38	4
11	11	2	18	43	2
18	11	2	18	43	2
11	11	4	18	56	2
18	11	4	18	55	2
warm temp. controls	18	-[a]	18	107[b]	2
	11	-[a]	11	137+[b]	2

[a]Continuous treatment under designated photoperiod.

[b]Total heading time from planting minus the 63 days that the vernalized plants were germinating and under cool temperatures.

However, a similar effect of cool-short photoperiods was obtained in Experiment 10, conducted a year later.

Experiment 10 This experiment was designed to obtain further information on interactions of temperatures and photoperiods. The experiment was a 4x2x3 factorial with all treatment combinations of four varieties of wheat at two cool photoperiods and three subsequent warm photoperiods. The experimental design was a split-split-plot with warm photoperiods as the whole plots, cool photoperiods as sub-plots and varieties as sub-sub-plots. The warm photoperiods were replicated by using eight of the newly constructed photoperiod chambers described in the MATERIALS AND METHODS. The cool photoperiods were replicated for about 6 weeks by using a pair of partially-heated cold frames outdoors. These were abandoned, however, when the temperatures within dropped to 29° F. during sub-zero weather. The 24 treatments were replicated four times, but because of space shortage replications 1 and 2 were planted on November 23, 1956, and replications 3 and 4 were planted 2 weeks later. At each of the two dates 12 pots were planted of each of the four varieties, Harvest Queen, Pawnee, Turkey, and Minter, and after germination and thinning these were equally distributed according to plan between the two cool photoperiod compartments. After 12 weeks of cool temperatures, replication 1 was transferred to the warm temperatures and either 13-, 14-, or 18-hour photoperiods.

Replication 2 received 13 weeks of cool temperatures and replications 3 and 4 received a total of 14 weeks of cool temperatures before transfer to warm temperatures. The short photoperiod at the cool temperatures became as long as 12 hours at the time replications 3 and 4 were transferred.

Dates of awn emergence and the numbers of spikelets per head were obtained from all the plants, and measurements of the final spike lengths were obtained in replications 3 and 4. The results are summarized in Table 21.

A striking acceleration of heading by 18-hour photoperiods during the cool temperature is evident from Tables 21 and 22 and Figure 8. With only two exceptions, plants on 18-hour photoperiods during the cool temperature headed several days earlier than those under 11 hours. The two exceptions were with Harvest Queen under 14 hours and Minter under 13 hours at warm temperatures. These two reversals of the general pattern are rather small and probably not significant. However, a similar effect was noted with Minter wheat in Experiment 3 where short photoperiods at the cool temperatures accelerated heading only when the plants were under inhibitory short days at the subsequent warm temperatures. It is also evident from Table 21 and the analysis of variance in Table 23 that short photoperiods during the cool temperatures encouraged the formation of more spikelets per head. Except under 13 hours at warm temperatures in the Minter and Harvest

Table 21. Effects of two photoperiods during cool temperature inductions and three photoperiods under subsequent warm temperatures on earliness of heading, spikelet formation and spike length of four varieties of winter wheat (Experiment 10)

Variety	Cool induction photoperiod[a] (hours)	Warm photoperiod	Time from end of cool temp. to awn emergence (days)	Final spike length (cm)	Number of spikelets per head
Harvest Queen	11	13	53	8.0	18.6
	18	13	44	9.7	13.0
	11	14	36	9.5	19.5
	18	14	37	7.8	14.4
	11	18	30	7.2	18.4
	18	18	26	6.2	15.0
Turkey	11	13	40	10.5	14.3
	18	13	29	8.0	12.5
	11	14	32	9.1	16.6
	18	14	25	6.7	11.3
	11	18	25	8.0	15.8
	18	18	19	6.9	12.5
Minter	11	13	49	9.8	19.3
	18	13	52	11.4	14.4
	11	14	37	8.9	18.9
	18	14	34	6.0	14.1
	11	18	30	7.8	16.4
	18	18	27	6.7	13.7
Pawnee	11	13	39	7.5	14.0
	18	13	29	7.1	12.0
	11	14	31	6.3	16.1
	18	14	23	6.5	12.4
	11	18	25	7.0	16.1
	18	18	21	5.7	12.6

[a]Cool induction treatments varied from 7 to 14 weeks for the four replications.

Table 22. Analysis of variance of data in Table 21 (Time to awn emergence, Experiment 10)

Source of variation	D.f.	M.s.
Replications	3	11.57
Warm photoperiods (WP)	2	2207.32**
Error (a)	6	55.70
Cool photoperiods (CP)	1	622.72**
CP x WP	2	17.36 N.S.
Error (b)	9	28.96
Varieties (V)	3	727.30**
V x WP	6	73.28*
V x CP	3	62.86 N.S.
V x CP x WP	6	35.64 N.S.
Error (c)	52[a]	26.64

[a]Three missing values reduced Error degrees of freedom by three.

*Significant at 5 per cent level.

**Significant at 1 per cent level.

N.S. Not significant at 5 per cent level.

Table 23. Analysis of variance of data in Table 21 (Number of spikelets per head)

Source of variation	D.f.	M.s.
Replications	3	8.272
Warm photoperiods (WP)	2	3.515 N.S.
Error (a)	6	6.319
Cool photoperiods (CP)	1	352.666**
CP x WP	2	5.206 N.S.
Error (b)	9	13.514
Varieties (V)	3	4.854*
V x WP	6	4.031*
V x CP	3	3.111 N.S.
V x CP x WP	6	2.973 N.S.
Error (c)	52[a]	1.502

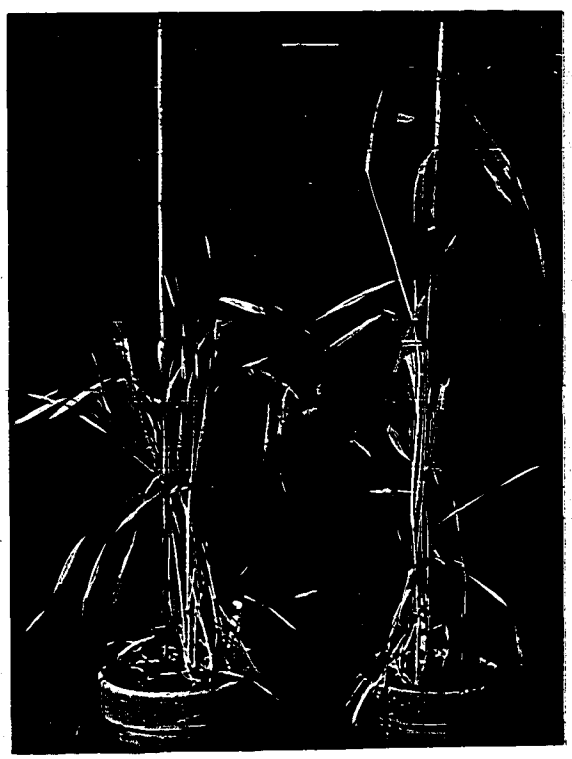
[a]Three missing values reduced Error degrees of freedom by three.

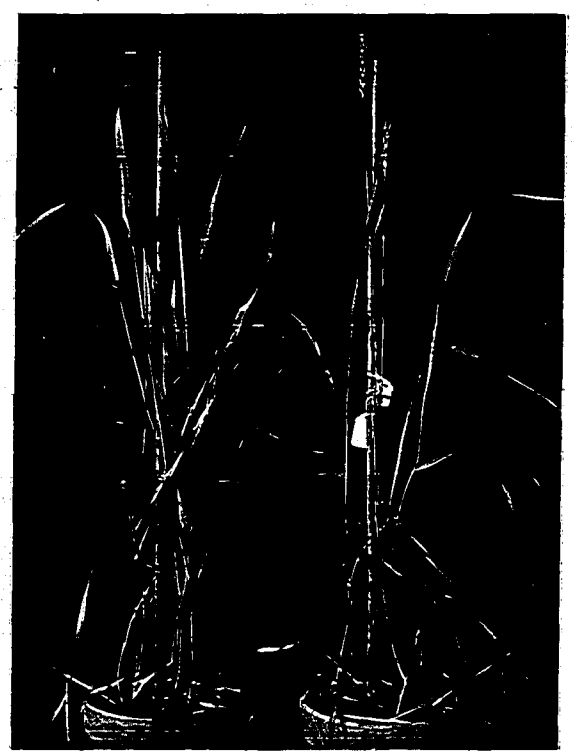
*Significant at 5 per cent level.

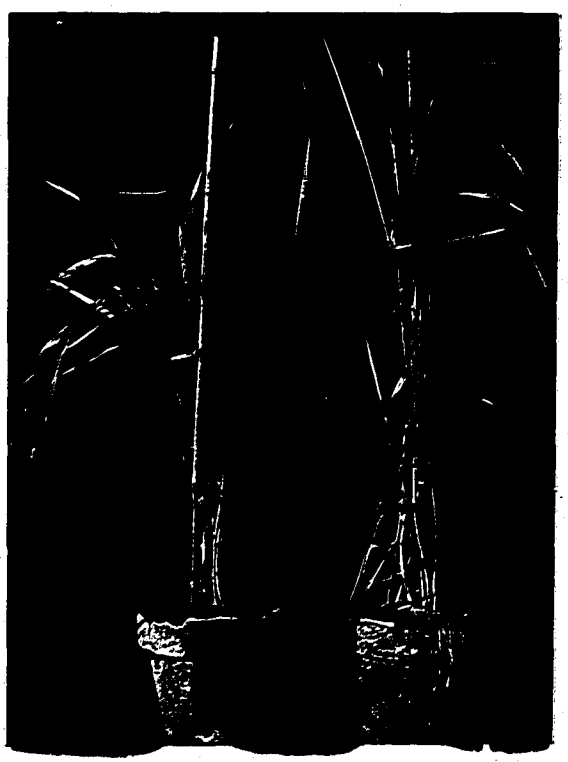
**Significant at 1 per cent level.

N.S. Not significant at 5 per cent level.

Figure 8. Effects of photoperiod during 12 to 14 weeks of cool temperature on development of wheat under subsequent warm temperatures. Plants at left in each photograph were under 11 hours at cool temperatures. Plants at right in each photograph were under 18 hours. Left photograph: Minter wheat (13-hour days) Right photograph: Turkey wheat (18-hour days) Center photograph: Harvest Queen wheat (13-hour days)







Queen varieties short photoperiods during the cool temperatures also increased final spike lengths. Other workers have reported that cool-short photoperiods increase the number of spikelets and the spike lengths formed under subsequent, warm-long photoperiods (42, 59). The general acceleration of heading by long photoperiods during long periods of cool temperature similar to that observed in Experiment 2 may be accounted for by assuming that the cool temperature reactions had been completed and the long photoperiods accelerated the photoperiodic induction reactions following. Initiation was inhibited by the cool temperatures, however, and had not occurred when the plants were transferred to the warm temperatures.

Experiment 17 An evaluation of the effects of photoperiod and plant age prior to cool-temperature treatment was desired. A total of five pre-treatments was imposed before transfer of the Minter wheat plants to the cool temperatures on February 8, 1957. The pre-treatments were as follows: 1, 2, 4, or 11 weeks of growth after planting under 18-hour photoperiods and 4 weeks of growth after planting under 11-hour photoperiods. The 1-, 2-, and 4-week pre-treatments were replicated 5 times and the 11-week pre-treatments were replicated twice. Following a uniform cool-temperature treatment of 7 weeks, the plants were returned to warm temperatures

and 18 hours. Heading and anthesis data were obtained and are summarized in Table 24.

The effect of the 11-hour pre-treatment photoperiods as compared with 18-hour photoperiods was to accelerate awn emergence an average of 3 days and anthesis an average of 2 days. As shown in Table 25 this difference was statistically significant. It also supports the findings in Experiment 2, where short photoperiods promoted floral induction when applied during warm temperatures.

In addition to the promotion of induction by short photoperiods there was a significant effect of increasing plant age in accelerating heading after the cool temperatures. Plants which were 4 weeks old and with 5 leaves before the cool-temperature treatment headed 3 days earlier than the 2-week-old plants with 3 leaves and 4 days earlier than the 1-week-old plants with 1 to 2 leaves. The plants that were 11 weeks old at the start of the cool induction period headed as early as the plants which received a 4-week short-day pre-treatment. The "11 week" plants suffered more under the cool temperatures than the younger plants by loss of leaves and chlorosis, but the "11 week" plants recovered sufficiently to head earlier than the "5 week" plants previously held under warm-long photoperiods. These results support those from Experiment 14 in which plant age also modified the response to cool temperatures. However, an increase in plant age from 3 to 7 weeks prior to cool-temperature treatment in Experiment

Table 24. Effects of plant age and pre-treatment photoperiods on earliness of Minter wheat given 7 weeks of cool temperatures (Experiment 17)

Pre-treatment photoperiod at warm temperatures (hours)	Age of plant at start of cool-temperature treatment (wks.)	(leaves)	Time from end of cool temperature to awn emergence (days)	Time from end of cool temperature to anthesis (days)
11	4	5	27	32
18	4	5	30	34
18	2	3	33	37
18	1	1-2	34	38
18	11	-	27	31

Table 25. Analysis of variance of data in Table 24 (Days to awn emergence)

Source of variation	D.f.	M.s.
Replications	4	4.58
Treatments	3	51.75**
4 weeks long vs. 4 weeks short	1	19.6*
4 weeks vs. 1 and 2 weeks	1	387.4**
Error	12	3.42

*Significant at 5 per cent level.

**Significant at 1 per cent level.

2 failed to modify the response and led to the conclusion that the effects of plant age probably reached a maximum within 3 weeks after planting. More work needs to be done in this direction before a definite conclusion can be reached. The findings in Experiments 2 and 14 would support the theory that the products of warm temperature induction and cool temperature induction were partially additive.

Photoperiod effects after cool temperatures

According to the literature (16, 32, 59, 67), winter wheat and rye behave as long-day plants following vernalization and dark periods are not essential. A total of nine separate experiments were designed to determine the effects of photoperiod on Minter wheat after vernalization. In addition to studies on Minter, three other varieties were included in Experiment 10. The main object of these experiments was to obtain more information on comparative photoperiod effects during every phase of floral development from the end of a vernalization treatment to heading. Effects of photoperiod on anthesis and seed set were not studied in general because previous work had indicated that these phenomena were quite sensitive to environmental factors other than photoperiod.

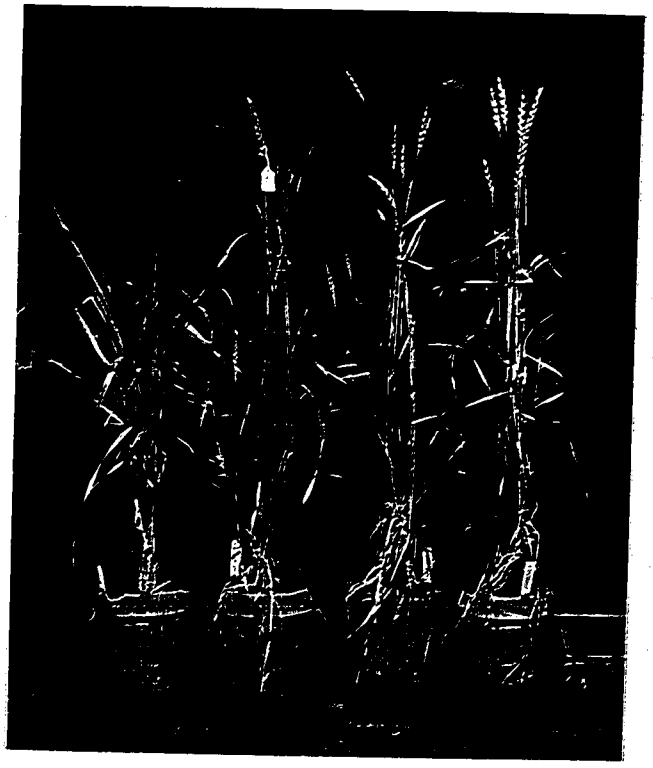
Experiment 3 The results of Experiment 3 which pertain to photoperiod effects during cool temperature induction were presented in the previous section. Plants of the variety

Minter were exposed to 11 or 18 hours for 6 weeks at the cool temperatures and then were transferred to 75° F. temperatures and either 11- or 18-hour photoperiods. In addition, a group of plants were held under 11 or 18 hours at warm temperatures continuously from planting. The six treatments imposed on the plants from each cool photoperiod were as follows: 2 weeks under 11 or 18 hours and then transfer to the opposite photoperiod, 4 weeks under 11 or 18 hours and then transfer to the opposite photoperiod, and 11 or 18 hours continuously. The results of the heading data obtained under the final photoperiods are summarized in Table 20.

The heading times for the two warm temperature controls shown at the bottom of Table 20 were calculated for comparison with the vernalized plants. The unvernalized plants held under 18 hours headed in 170 days after planting or 107 days after the comparable vernalized plots were transferred to the warm temperatures. The continuous short-day, unvernalized plants which actually were on natural long days for the last 2 months had not headed within 200 days of planting or 137 days after the vernalized plants were transferred to the warm temperatures. It is obvious from these figures and those in Table 20 that a combination of no cool-temperature treatment and short photoperiods severely delayed heading. These effects are illustrated in Figures 9 and 10. Continuous short days following cool induction delayed heading to between 109 and 118 days after the cool temperatures and these plants

Figure 9. Effects of cool temperature and subsequent photoperiod on development of Minter wheat. Left to right: (a) Warm temperatures and 11 hours continuously; (b), (c) and (d) 6 weeks of cool temperatures followed by various photoperiod treatments at warm temperatures: (b) 11 hours continuously, (c) 2 weeks at 18 hours then 11 hours, (d) 18 hours continuously.

Figure 10. Effects of photoperiod at warm temperatures on development of Minter wheat after cool temperatures.
Left to right: (a) Eleven hours continuously; (b) 2 weeks at 18 hours then 11 hours; (c) 4 weeks at 18 hours then 11 hours; (d) 18 hours continuously.



headed at about the same time as the continuous warm temperature controls. The delay on short days after vernalization might be considered devernalization, but as shown in Table 20 and in other data, when vernalized plants on short days were transferred to long days they completed their development quite rapidly. Short days merely slowed down the floral development process, therefore. Long photoperiods, on the other hand, appeared to accelerate heading whenever they were applied in development after cool temperatures.

What was desired, however, was to be able to evaluate more fully the short-day effects during the times they were applied. It was found that the breakdown of the number of days from the end of the cool-temperature treatment to awn emergence allowed a computation of the average effectiveness of the 11-hour photoperiods relative to the effectiveness of the 18-hour photoperiods. The effectiveness of a photoperiod was assumed to be inversely proportional to the number of days to heading. Therefore, by further assuming that the effectiveness of an 18-hour photoperiod was unity, it was possible to calculate the "relative effectiveness coefficients" of any other photoperiod treatments during the times they were applied. In experiments where the photoperiod treatments are continuous to heading, the average effectiveness of any given photoperiod treatment is obtained by simply dividing the number of days required for the plants to head under

continuous 18-hour photoperiods by the number of days required for the plants to head under the given photoperiod as follows:

$$K = \frac{MHT}{SD}$$

where K = the "relative effectiveness coefficient" the effectiveness of any given photoperiod relative to the effectiveness of 18-hour photoperiods.

SD = the number of days of the given photoperiod that were applied from the beginning of photoperiod treatment.

MHT = the number of 18-hour days required from the beginning of the photoperiod treatment to heading, i.e., the minimal heading time.

In the above computation it is assumed that the SD plants remained under the given photoperiod continuously to heading. However, when the photoperiod treatments involved a transfer of plants from 18-hour photoperiods to another photoperiod or vise versa, as was the case in Experiment 3, it was necessary to devise a special formula to compute the "effectiveness" of the other photoperiods relative to the effectiveness of 18-hour photoperiods.

Thus, $K \times SD + LD = MHT$

$$\text{or } K = \frac{MHT - LD}{SD}$$

where LD = the number of 18-hour days applied from the beginning of the photoperiod treatment.

As the average effectiveness of a given photoperiod treatment approaches that of the 18-hour photoperiod, the value K approaches 1. In Experiment 3 the photoperiod being compared with 18 hours is 11 hours, but a similar procedure could be used for any photoperiod treatment.

The following method was then used in Experiment 3. The heading times for each post-vernalization treatment in Table 20 were averaged over both cool photoperiods and arranged in the manner illustrated in Table 26, such that the number of short days and the number of long days for each treatment were readily obtained. From these values the "effectiveness coefficients" of the short days applied during each of the treatments were computed and are also shown in Table 26. These "effectiveness coefficients" point out, first of all, that the 11-hour photoperiods when applied continuously were only about one-third as effective in accelerating heading as were 18-hour photoperiods. The same was true when the short days were applied for more than 2 weeks preceding long days or following only a 2-week period of long days. However, the short days were more effective or less inhibitory relative to the 18-hour days when applied just after the cool temperature, or following a 4-week period of 18-hour days. For the 2-week period following the cool temperatures, the average effectiveness of an 11-hour day was 0.57 times the effectiveness of a corresponding 18-hour day whereas the average effectiveness of the short days applied after 4 weeks of long days was 0.69

Table 26. Effectiveness of 11-hour photoperiods applied during different times in the development of Minter wheat from vernalized plants (data from Experiment 3, Table 20)

	Total days from end of vernalization to awn emergence[a]	Number of 11-hour days (SD)	Number of 18-hour days (LD)	Relative effectiveness[b]
Short days preceding periods of long days	43	14	29	0.57
	56	28	28	0.32
	114	114	0	0.32
Short days following periods of long days	78	64	14	0.36
	41	13	28	0.69
	37[c]	0	37	

[a]Averaged over both cool photoperiods in Table 20.

[b]Relative effectiveness of 11-hour photoperiods $= \frac{MHT-LD}{SD}$

[c]MHT (minimal heading time) = 37 days in this experiment.

times that of the 18-hour day. Early development following cool temperatures and late floral development were, therefore, less sensitive to photoperiod than the intermediate periods. Further information of this type was sought in Experiment 7, conducted a year later.

Experiment 7 Much of this experiment resembled Experiment 3 but several modifications were made to obtain more information on photoperiod effects following the cool temperatures. Therefore, instead of vernalizing the plants, seeds were planted which had been vernalized at 1° C. for 9 weeks prior to planting. Although an attempt had been made to replicate photoperiods in Experiment 3 by the use of a pair of closed compartments, this had failed and these compartments were discarded. During the summer of 1956 the photoperiod chambers were built that are described in the MATERIALS AND METHODS and illustrated in Figure 4. One of the three replications of Experiment 7 was then held in these chambers. An added feature also was the sampling of plants under both photoperiods and an increase in the number of transfers to opposite daylengths.

The vernalized seeds of Minter wheat were planted in 66 5-inch pots on October 13, 1956 and the pots were held under natural light conditions for 6 days. At this time the plants were thinned uniformly to two per pot and the pots divided into three replications of 22 pots each. Eleven pots from each replication were placed under 11- or 18-hour photoperiods and six treatments were randomly assigned to the 11 pots as follows: initial photoperiod continuously or initial photoperiod for 1, 2, 3, 4, or 5 weeks, then transfer to the opposite photoperiod. At each of the dates of transfer to the

opposite photoperiod, the plants of the five remaining pots of the initial 11 were harvested for dissection. The number of days from planting to awn emergence was obtained for the main tillers of each of the plants that were not harvested and the data obtained on the main tillers of harvested plants were as follows: (a) the numbers of visible leaves, (b) the stages of development of the apex, (c) the numbers of spikelet primordia, and (d) the spike lengths. The results for both the initiation data obtained from the harvested plants and the heading data are summarized in Table 27 and the analysis of variance is given in Table 28. The initiation data, therefore, indicate the development of the plants under the initial photoperiod at the time they were transferred to the opposite or final photoperiod.

From Table 27 it is evident that the production of leaves was independent of daylength but floral development was much more rapid under 18-hour days than under 11-hour days. The plants on long days started initiating spikelet primordia within 3 weeks after planting whereas the short-day plants were just beginning to initiate primordia at 6 weeks from planting. From this experiment and many other dissections, spikelet initiation appeared to occur when the spikes were between 0.6 and 0.9 mm in length.

Rapid exponential growth of the spikes occurred in the long-day plants after initiation but did not occur in the

Table 27. Effects of 11- and 18-hour photoperiods on spikelet initiation and earliness of heading of vernalized Minter wheat (Experiment 7)[a]

Initial photoperiod and duration (hrs.)	(wks.)	Final photoperiod (hrs.)	Initiation data taken at time of transfer to final photoperiod: Number visible leaves	Spike length (mm)	Stage[b]	Number of spikelet primordia	Time of heading[c] (days)
11	1	18	3.1	-	1.0	0	50
11	2	18	4.2	-	1.0	0	56
11	3	18	5.3	-	1.0	0	65
11	4	18	6.8	0.54	1.0	0	66
11	5	18	7.0	0.64	1.3	0	68
11	continuous	11	-	-	-	-	124
18	1	11	3.2	-	1.0	0	111
18	2	11	4.7	0.98	3.0	5.2	95
18	3	11	5.2	1.63	5.0	11.6	79
18	4	11	7.2	5.68	6.7	14.0	57
18	5	11	7.7	19.91	7.8	14.3	49
18	continuous	18	-	-	-	-	47

[a]All figures are an average of three replicates of two plants each. A 6-day period elapsed between planting and start of treatments.

[b]Stage of development of apex.

[c]Time from planting to awn emergence.

Table 28. Analysis of variance of data in Table 27 (Days from planting to awn emergence)

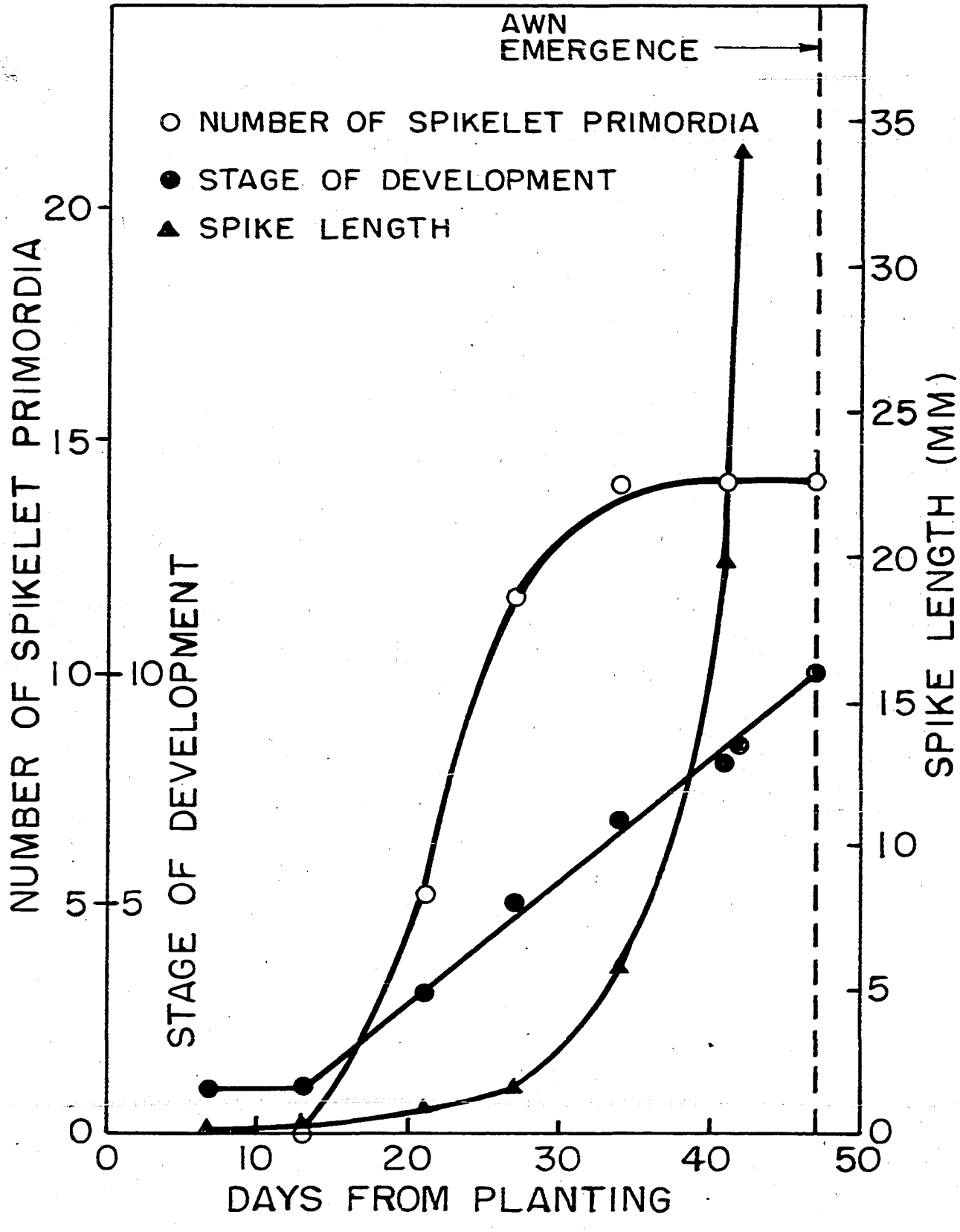
Source of variation	D.f.	M.s.
Replications	2	96.81**
Treatments	11	1907.25**
Error	22	62.76

**Significant at 1 per cent level.

short-day plants within 6 weeks. Gott, Gregory and Purvis (32) reported that the growth rate of spikes of vernalized rye under 8- or 10-hour days increases gradually but does not reach a rapid exponential level up to 19 weeks after planting.

The relationships among the rates of increase of spike length, numbers of spikelet primordia, and stages of development of vernalized wheat grown under long days are shown in Figure 11. The data were obtained from Experiment 7 and from preliminary experiments. It is seen that after initiation the increase in stages of floral development proceeded almost linearly with time whereas the numbers of spikelet primordia leveled off sometime before awn emergence. For this reason, the number of spikelet primordia alone is a poor criterion for use in evaluating floral development in the later stages. Spike length, on the other hand, increases exponentially

Figure 11. Variation in apical growth and development of Minter wheat with time after planting under 18-hour photoperiods and warm temperatures.
Plants were from seeds vernalized for 9 weeks at 1° C.


AWN
EMERGENCE
NUMBER OF SPIKELET PRIMORDIA
STAGE OF DEVELOPMENT
SPIKE LENGTH
NUMBER OF SPIKELET PRIMORDIA
STAGE OF DEVELOPMENT
SPIKE LENGTH (MM)
DAYS FROM PLANTING
0
5
10
15
20
25
30
35
40
50

after initiation but has been shown by Chinoy and Nanda (15) to be highly correlated with the subsequent time to heading. Gott, Gregory and Purvis (32) reported that spike length was affected by nitrogen application but the spike development "score" as they used it was not. However, this would be an important consideration only in making comparisons among plants of different experiments or where varying nitrogen applications were being made in the same experiment. Spike measurements are accurate and rapid while any scoring method is time consuming.

The heading data of Experiment 7, also shown in Table 27, indicate again the relatively inhibitory effects of 11-hour photoperiods on floral development. To properly evaluate the average effects of the short photoperiods during the times they were applied, however, it is advantageous to compute the "effectiveness coefficients" as in Experiment 3. As pointed out in Table 29, the 6-day period during seedling emergence prior to the start of the photoperiod treatments was subtracted from the total days from planting to heading for each treatment.

The average effectiveness of a short-day treatment decreased with increase in time of short-day application following planting, and it increased with an increase in the number of long days before short-day application. Similar results were obtained in the previous Experiment 3. However, in

Table 29. Effectiveness of 11-hour photoperiods applied during various stages in the development of vernalized Minter wheat (Data from Experiment 7, Table 27)

	Total days from planting to awn emergence[a]	Number of 11-hour days (SD)	Number of 18-hour days (LD)	Relative effectiveness[b]
	44	7	37	0.57
Short days preceding periods of long days	50	14	36	0.36
	59	21	38	0.14
	60	28	32	0.36
	62	35	27	0.40
	115	115	0	0.35
	105	98	7	0.35
Short days following periods of long days	89	75	14	0.36
	73	52	21	0.38
	51	23	28	0.57
	43	8	35	0.75
	41[c]	0	41	-

[a]Neglecting 6-day period during seedling emergence.

[b]Relative effectiveness of short days = $\frac{MHT-LD}{SD}$

[c]MHT (minimal time to heading) = 41 days in this experiment.

Experiment 7, it was possible to relate data from the harvested plants (Table 27) with the average relative effectiveness of short photoperiods following (Table 29). The effectiveness of the short photoperiods did not increase appreciably until after 4 weeks of long days or when the spikelets had advanced to about stage 7 and were almost 6 mm long. At this time all the spikelet primordia had been differentiated, and further increase in the number of spikelets would not be expected after this stage, even under short days. It can be concluded, therefore, that the floral development of plants was delayed more by short days applied before initiation of all the spikelet primordia than by the same short days applied after this. In certain supporting experiments, plants which had advanced to between stages 7 and 8 were delayed slightly or not at all by short photoperiods following. Thus, further floral development, after initiation, is less sensitive to photoperiod. The effect of short days, then, is hardly constant throughout the development process.

The relatively high "effectiveness coefficients" for short days immediately following planting or removal of plants from cool temperatures suggest that the photoperiodic reactions are not very active until there is a minimum period allowed for increase of the vernalization product. This time period required for increase may well be manifested in the

production of the minimum number of leaves, found in Experiment 1 to be about five.

Experiment 19 In Experiment 7 the plants had emerged from the soil and had developed one or two visible leaves before being transferred to the two photoperiods. The effect of photoperiod immediately after emergence still remained to be determined. Experiment 19 was designed to fulfill this purpose. Twenty-one 6-inch pots of vernalized seed were sown on March 22, 1957. The seed had been vernalized at 1° to 2° C. for 51 days. Immediately after the seeds were sown, nine pots were placed under 11-hour photoperiods, six pots were placed in an 18-hour compartment and the remaining six pots were placed under the greenhouse bench and covered to exclude light. Three pots were removed from each position at 7 and 11 days and placed under continuous light. At 17 days the remaining three pots were removed from the 11-hour photoperiod compartments and also placed under continuous light. At the time of transfer, the plants were thinned to two per pot and counts were made of visible leaf numbers. The plants held in darkness were almost devoid of color but had a total of two visible leaves at 7 days and three leaves at 11 days after planting. The same number of visible leaves was produced under 11- and 18-hour photoperiods during these two periods. At the 17-day removal of plants from 11 hours, however, four leaves were externally visible.

The times from planting to awn emergence for all treatments are shown in Table 30 and the analysis of variance is given in Table 31. Photoperiod during the first 7 or 11 days after planting appeared to have little effect on the time of awn emergence under subsequent continuous illumination. Plants receiving 11 days of darkness or 18 hours of light headed in 40 days while those under 11-hour photoperiods headed in an average of 41 days. According to the analysis of variance in Table 31, the difference between 7 and 11 short-day treatments is probably significant but of no great importance, because the 18-hour photoperiods for 11 days caused heading to occur only 1 day earlier than 11-hour photoperiods for the same duration. The important point is that photoperiod did not appear to be an important factor in floral development during this early period. This accounts for the high "effectiveness coefficients" obtained for short days during the first 13 days after planting in Experiment 7.

Experiment 10 The effects of three post-vernalization photoperiods on earliness of heading and spike development of varieties of winter wheat were studied in Experiment 10. This experiment also involved photoperiod treatments during the cool temperatures and has been described in detail in the preceding section, Photoperiod effects prior to and during cool temperatures. One of the objects of the post-vernalization photoperiods in this experiment was to determine

Table 30. Effects of photoperiods immediately following planting of vernalized Minter wheat on the time of awn emergence under subsequent continuous light (Experiment 19)

Photoperiod (hours)	and duration (days)	Time from planting to awn emergence (days)
11	7	38
11	11	41
11	17	46
0[a]	7	39
0[a]	11	40
18	7	39
18	11	40

[a]Darkness.

Table 31. Analysis of variance of data in Table 30 (Days from planting to awn emergence)

Source of variation	D.f.	M.s.
Replications	2	2.630
Treatments	6	19.926**
11 hours, 17 days vs. others	1	99.020**
Among others	5	4.100*
Error	11[a]	1.113

[a]One missing value reduced Error degrees of freedom by one.

*Significant at 5 per cent level.

**Significant at 1 per cent level.

the differential response of the four varieties to intermediate and long photoperiods after a uniform cool-temperature treatment. The four varieties, Harvest Queen, Turkey, Minter, and Pawnee, were used. As described earlier, the experiment was a three-factor factorial will all combinations of two cool photoperiod treatments of 11 or 18 hours, the four above-mentioned varieties and three post-vernalization photoperiods of 13, 14, or 18 hours. Data were obtained on the following: (a) the times from the end of the cool temperatures to awn emergence, (b) the final spike lengths, and (c) the number of spikelets per head. The results are summarized in Table 21.

In each of the four varieties the times to heading decreased with increase in the post-vernalization photoperiods. However, there was a significant warm photoperiod x variety interaction as shown in Table 22. Harvest Queen and Minter were later maturing at all three photoperiods than Pawnee and Turkey, but the greatest difference was under the 13-hour photoperiods.

Spike lengths appeared to decrease generally with an increase in the length of the photoperiod. The longest spikes usually were produced under the 13- and 14-hour photoperiods. However, cool photoperiods appeared to have greater effects than post-vernalization photoperiods on both spike lengths and the number of spikelets formed per head. Spikes with

greatly elongated bases often were produced under the shorter photoperiods and were most common under 13-hour photoperiods.

The later heading varieties (Harvest Queen and Minter) produced larger numbers of spikelets per head; and, as indicated in Table 23, the differences among varieties were significant. Many of the spikelets produced under all photoperiods were small and sterile, however. There were no significant differences among the post-vernalization photoperiods in the production of spikelets, although there was a significant variety x warm photoperiod interaction. Minter produced more spikelets than Harvest Queen under 13-hour photoperiods and considerably less under 18-hour photoperiods.

It is well known that winter wheat varieties differ widely in their flowering response to different photoperiods. In general, however, long photoperiods after vernalization accelerate heading and tend to decrease spike lengths. For this reason, vernalized plants held on long days continuously do not produce the yields that plants do on slowly increasing daylengths.

Experiment 9 The effects of daily alternation of long and short photoperiods on earliness of heading of Minter wheat was investigated in a single experiment conducted during the 1956-57 season. Seeds which had been vernalized for 8 weeks at 1° C. were sown in nine 5-inch pots on October 13, 1956.

After six days the plants were uniformly thinned to two per pot and the daily alternation of photoperiods was started. Three of the nine pots were moved every morning to the opposite photoperiod, either 11 or 18 hours, and three pots were held as controls under each of the two photoperiods. The times from planting to awn emergence were obtained for the main tillers of each plant. The relative "effectiveness coefficients" of the short photoperiods were calculated from the number of short and long days to heading as described in Experiment 3. As before it was assumed that the effectiveness of an 18-hour day was unity regardless of its time of application.

In Table 32 the 6 days involved in starting the seedlings were subtracted from the times from planting to awn emergence, which gives the time from seedling emergence to heading. The daily alternations of short and long days shortened the time of heading from 125 days for the plants under continuous short days to 58 days. The continuous 18-hour plants headed in 38 days. The interesting point is that the effectiveness of the short days was the same whether the short days alternated with long days or whether they were applied continuously. In either case, short days were only about one-third as effective as long days in promoting heading of Minter wheat. This value can, therefore, be taken as an overall average estimate of the relative effectiveness of 11-hour photoperiods.

Table 32. Relative effectiveness of 11-hour photoperiods during daily alternation of 11- and 18-hour photoperiods (Experiment 9)

Treatment	Total days from seedling emergence to heading	Number of 11-hour days (SD)	Number of 18-hour days (LD)	Relative effectiveness[a]
11 hours	125	125	0	0.30
Daily alternating 11- and 18-hour photoperiods	58	29	29	0.31
18 hours	38[b]	0	38	

[a] Effectiveness = $\frac{\text{MHT-LD}}{\text{SD}} = \frac{38 - 29}{29} = 0.31$.

[b] MHT (minimal heading time) = 38 days.

Experiment 6 In order to study further the relative effects of different photoperiods, Experiment 6 was initiated during the fall and winter of 1956-57. The experiment consisted of three parts, all conducted with seeds of Minter wheat which had been vernalized at 1° C. for 8 weeks prior to planting.

The specific purpose of Part A was to determine effects of varying photoperiods on spikelet initiation. In Part B, the purpose was to evaluate photoperiod effects on complete floral development, and floral development following initiation was studied in Part C. The plants were exposed to four

different photoperiods of 11, 13, 15.5, and 18 hours. The 13 and 15.5 photoperiods were selected because they were intermediate between 11 and 18 hours. Eight compartments were available at one time. To avoid having more than one replication in the same compartment only two replications were started on a given date and the others followed at later dates.

In Part A the seedling plants were placed under the four photoperiods immediately. They were harvested at 5 weeks from planting, and measurements were made of visible leaf numbers, numbers of tillers, fresh weights of tops, spike lengths, numbers of spikelet primordia and stages of floral development. In Part B, the plants were held under the four photoperiods until heading and the numbers of days from planting to awn emergence and anthesis were obtained. In Part C, the plants were held on 18-hour photoperiods for 5 weeks and then were transferred to the four photoperiods for further development. Dates of awn emergence and anthesis were recorded. Part A was replicated 5 times, Part B, four times, and Part C, three times.

The results for Part A, as outlined in Table 33, indicate that there were no large differences in leaf numbers and fresh weights of the plant tops among the plants under the four photoperiods. As was found in other experiments, the 11-hour photoperiods produced more than twice as many tillers as the other photoperiods. The observations on floral

Table 33. Effects of four photoperiods on growth and spikelet initiation of vernalized Minter wheat harvested 5 weeks after planting (Experiment 6, Part A)[a]

Photoperiod	No. of visible leaves	Fresh wgt. tops (gms)	No. of tillers	Spike length (mm)	No. of spikelet primordia	Stage[b]
11	6.9	3.99	2.7	0.41	0	1.0
13	6.4	2.79	1.0	0.51	0	1.1
15.5	6.9	3.45	1.0	1.50	10.5	5.1
18	6.6	3.03	1.3	2.33	14.5	6.6

[a]Figures are an average of five replicates of two plants each.

[b]Stage of development of apex.

development also pointed out clear-cut differences among the photoperiods. Whereas the spikes of the 11- and 13-hour plants were mostly less than 0.5 mm and had produced no visible floral primordia, the spikes of the 15.5- and 18-hour plants were three to five times longer and many spikelet primordia were in evidence. As shown in Table 34, the differences in spike lengths were significant at the 1 per cent level. In Experiment 7, spikelet differentiation was just beginning at 5 weeks after planting in plants under 11-hour photoperiods. Observations from preliminary experiments also indicated that under 11-hour photoperiods initiation

Table 34. Analysis of variance of data in Table 33 (Spike lengths)

Source of variation	D.f.	M.s.
Replications	4	0.147
Photoperiods	3	4.104**
Error	12	0.074

**Significant at 1 per cent level.

occurs between 5 and 7 weeks after planting. Gott, Gregory and Purvis (32) have reported an interaction of vernalization duration and time of initiation of rye, as would be expected. Therefore, the time initiation of spikelet primordia is first noticed depends to a great extent upon the degree of vernalization of the seeds or plants.

The plants of Part B were allowed to mature under the four photoperiods and the results of the heading data are shown in Table 35. None of the plants under 11 hours headed within 158 days from planting and only four of the 13-hour plants headed within that time. The average heading time of the four plants that did head under 13 hours was 101 days, while the 15.5-hour plants and the 18-hour plants headed in only 69 and 56 days, respectively. The severe delay of heading under 13 and 11 hours was not considered normal because

Table 35. Effects of four photoperiods on earliness of heading of vernalized Minter wheat grown on these photoperiods from the seedling stage (Experiment 6, Part B)

Photoperiod	Days from planting to awn emergence
11	-[a]
13	101[b]
15.5	69
18	56

[a]No plants headed 158 days from planting.

[b]Only two of four replicates headed 132 days from planting.

results from Experiment 7 in which the plants were grown in the same area showed that heading occurred under 11-hour photoperiods within 130 days from planting. It is possible that the higher (80° to 90° F.) temperatures prevailing during the early phases of Experiment 6, Part B resulted in undue delay of heading under the less optimum photoperiods. From the results of Parts A and B, however, it was confirmed that both initiation and the complete floral development of Minter wheat were promoted by increasing photoperiods.

In Part C the plants had received a total of 5 weeks of 18-hour photoperiods before transfer to the four photoperiods. According to the findings in Part A (Table 33), these plants

should have initiated several spikelet primordia by the date of transfer. The results summarized in Table 36 were obtained under the four photoperiods. Incomplete data were

Table 36. Effects of four photoperiods on heading of vernalized Minter wheat after 5 weeks of 18-hour photoperiods (Experiment 6, Part C)[a]

Photoperiod (hours)	Time from planting to awn emergence (days)	Time from planting to anthesis (days)	Time from transfer to awn emergence (days)	Relative effectiveness of final photoperiod[b]
11	135	-	100	0.19
13	68	-	33	0.58
15.5	55	60	20	0.95
18	54	59	19	1.00

[a]Figures are an average of three replicates of two plants each.

[b]Relative effectiveness based on times from transfer to awn emergence = $\frac{\text{No. 18-hour days}}{\text{No. days for another photoperiod}}$

obtained on times of anthesis because of the irregular heading of the 11- and 13-hour plants. Under the shorter photoperiods the spikes often failed to emerge normally from the boot, and the determination of the time of first anther extrusion was, therefore, impossible.

The data on times to awn emergence point out the relatively inhibitory effects of short photoperiod on further floral development. The analysis of variance of the heading data, shown in Table 37, confirms the significance of these

Table 37. Analysis of variance of data in Table 36

Source of variation	D.f.	M.s.
Replications	2	119.08
Photoperiods	3	4486.33**
Error	6	257.75

**Significant at 1 per cent level.

differences. The relative "effectiveness coefficients" were computed for the 11-, 13-, and 15.5-hour photoperiods using the average heading time of the 18-hour photoperiods as the minimal heading time. Because only the final photoperiods were of interest, the data on times from transfer to awn emergence were used in the computation. The method of computation was described in Experiment 3. The results in Table 36 show that the effectiveness of the 15.5-hour photoperiods was almost equal to that of the 18-hour photoperiods, but the

11-hour photoperiods were even less effective relative to 18-hour photoperiods than had been determined in Experiments 3, 7, and 9. As with initiation and complete floral development, further floral development following initiation also is accelerated by increasing lengths of day, but according to results obtained in Experiments 3 and 7, the daylength effects are greater before initiation has begun.

Experiment 12 Although there was little doubt as to whether the floral responses of vernalized Minter wheat were those of a long-day plant, a small experiment was conducted during the 1956-57 season to determine the effects of night interruption on floral development. Other photoperiod treatments were included as comparisons. The five photoperiods used were 11, 13, 15.5, and 18 hours and 11 hours plus a 2-hour light period in the middle of the dark periods. The plants used were all from Minter seeds vernalized for a minimun of 7 weeks at 1° C. A total of seven replications of the five photoperiod treatments were planted at different times, although the plants within each replication were uniform. As in all other experiments, the experimental unit was a single pot of two plants. Four of the replications were harvested for dissection at appropriate times to compare photoperiod effects on initiation. Observations were made of spike lengths and stages of development. The other three replications remained under the five photoperiods, and heading data

were obtained. Both the initiation and heading data are summarized in Table 38. The "relative effectiveness coefficients" were computed for both sets of data, using the stages of development and the times from planting to awn emergence. These coefficients also are shown in Table 38.

Table 38. A comparison of the effects of night-interrupted short days and four other photoperiods on spikelet initiation and time to heading of vernalized Minter wheat (Experiment 12)

	Initiation[b]			Heading[a]	
Photoperiod (hours)	Spike length (mm)	Stage of development	Rel. effect.[c]	Time from planting to awn emergence	Rel. effect.[d]
11+2 (in dark period)	0.94	6.7	3.45	65	0.86
11	0.30	2.1	0.55	149	0.38
13	0.54	3.8	0.69	111	0.50
15.5	0.94	6.7	3.21	74	0.76
18	1.00	7.1	5.02	56	1.00

[a]Figures an average of two to three replicates of two plants each.

[b]Figures an average of four to five replicates of two plants each.

[c]Relative effectiveness based on stages of development.

[d]Relative effectiveness based on days to heading.

The "effectiveness coefficients" increased generally with increase in photoperiod, excluding the night-interruption treatment. The spike lengths followed the same pattern. However, the addition of 2 hours of light during the middle of the dark period to an otherwise ineffective 11-hour day produced a promotive effect much greater than that of a 13-hour day even though the total hours of light were the same for the continuous 13 hours and 11 + 2 hours. This effect is illustrated in Figure 12. The 11 + 2-hour photoperiod treatment was 94 per cent as effective as 18-hour photoperiods in promoting initiation and 86 per cent as effective in promoting early heading. The effectiveness of the 11 + 2-hour photoperiod was similar to that of the 15.5-hour photoperiod. Because the promotive effects of 11 + 2 hours of light were much greater than the effects of 13 continuous hours of light, it is confirmed that the photoperiodic response of vernalized Minter wheat is typical of a long-day plant.

Experiment 16 The effects of continued short days on the vegetative and floral development of vernalized Minter wheat was determined in Experiment 16, conducted during the winter and spring of 1956-57.

On December 28, 1956, 30 6-inch pots were sown with seeds of Minter wheat which had been vernalized for 12 weeks at 1° C. The plants were held under 11- to 12-hour photoperiods

Figure 12. Effects of interrupting the dark period of vernalized Minter wheat.
Left to right: (a) 18-hour day, (b) 11-hour day plus 2 hours of light in middle of dark period, (c) 13-hour day.

until their final harvest or transfer to long photoperiods. When the plants were 5 weeks of age the observed elongation of the basal internodes indicated that the plants had started initiating spikelet primordia. Five pots were then transferred to 18-hour photoperiods and a count was made of the number of visible leaves. Five pots were removed from the short-day group at 7, 9, 11, 13, and 14 weeks after planting. At each of these times the plants of three pots were harvested and records were made of the numbers of visible leaves and spikelet primordia, the stages of development and the spike lengths. The other two pots were transferred to 18-hour photoperiods and records were obtained on the dates of awn emergence, the final number of leaves and spikelets and the spike lengths. All data were obtained on the main tillers of each plant. The results of observations on the harvested and the headed plants are shown in Table 39.

From the observations on the harvested plants, it can be seen that under continued short days the number of visible leaves increased from five to about eleven over a 9-week period. The average increase, therefore, was 1.5 leaves per week. The difference between the visible leaf numbers of the harvested plants and the final leaf numbers of the plants which headed under long days is rather interesting and, no doubt, is related to the time to heading on long days. This difference indicates the number of primordial leaves that

Table 39. Effects of short photoperiods (11-12 hours) of varying duration on spike development of vernalized Minter wheat before and after transfer to 18-hour photoperiods (Experiment 16)

Duration of short photoperiods (weeks)	Plants harvested after short photoperiod treatment				Plants allowed to head under 18-hour photoperiods			
	Visible leaves	Spikelet primordia	Stage[a]	Spike length (mm)	Final leaves	Number of spikelets	Spike length (mm)	18-hour days to heading
5	5.0	-	-	-	9.2	20.8	95	33
7	6.8	11.5	3.25	1.00	9.3	22.0	90	24
9	7.6	20.6	4.4	1.62	9.5	23.8	92	24
11	9.8	26.5	6.5	2.81	11.1	25.0	113	17
13	10.0	26.7	7.0	8.10	11.8	25.0	118	17
14	10.8	25.8	-	8.23	12.3	25.0	161	14

[a]Stage of development.

develop before heading finally occurs on long days. Therefore, as the number of primordial leaves indicated by this difference decreased, so did the times to heading.

The plants that were transferred to long days with an average of only 11.5 spikelet primordia in early stages of differentiation finally produced 22 spikelets before heading. However, the plants which already had initiated an average of 26.5 spikelet primordia with a stage of development rating of 6.5 did not produce any more spikelets after transfer to long days. There seems to be a stage in the differentiation of the spike after which no further spikelet increase occurs regardless of subsequent photoperiods.

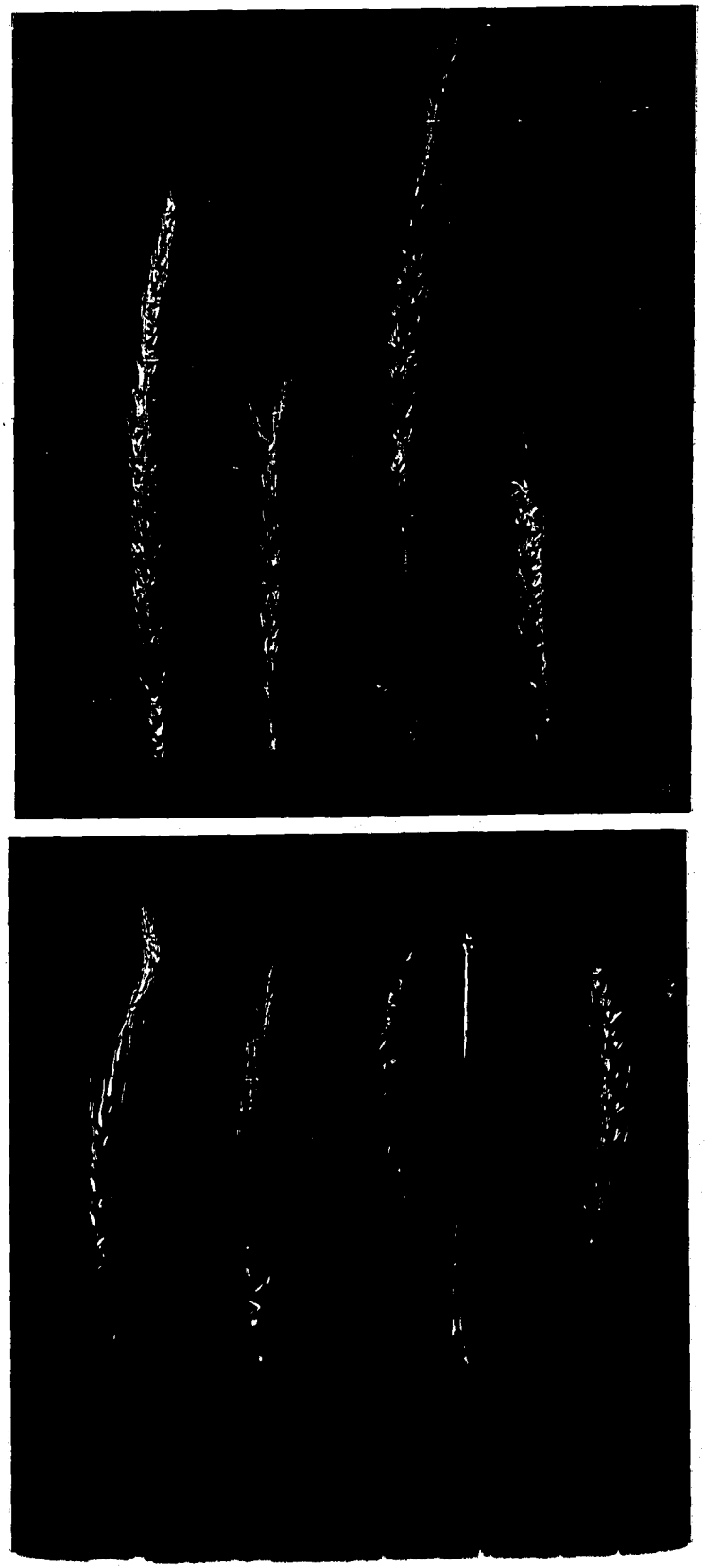
With increasing duration of short-day exposure, the spike lengths and numbers of spikelet primordia increased in the harvested plants. The increase in spike lengths appeared to be quite gradual until the 13th week when a three-fold increase in length was obtained over the 11th week. Since the plants would have been expected to head even on short photoperiods within 20 to 30 more days, the growth rates of the spikes might also be expected to increase as heading approached. Gott, Gregory and Purvis (32) concluded from their work with rye that the onset of the grand period of growth after initiation was dependent on the daylength. It was very rapid on continuous light, and absent on short days up to 19 weeks after planting.

The increased spike lengths of the plants which headed reflect both the increased number of spikelets formed on short days and the increased elongation of the basal internodes of the spikes. Although the numbers of spikelets did not increase in the headed plants after the 11th week, the spike lengths did increase as a result of internode elongation. Gott, Gregory and Purvis (32) reported that abnormal elongation was noted in rye only when the plants had begun initiation on long days before exposure to short days, but never after continuous short days (10 hours). However, abnormal spike elongation also occurred under 13-hour photoperiods in Experiment 11 where the only long photoperiods applied were during the cool-temperature treatments before initiation had taken place.

Also noted in some of the plants transferred from short to long photoperiods was the tendency for lower spikelets to form secondary spikes, as illustrated in Figure 13. The secondary spikes were characterized by elongated spikelets with an unusually large number of florets. Secondary spikes have been observed by several workers to occur in plants under threshold flowering conditions (32, 70, 77).

Another common heading abnormality observed quite frequently in plants removed from short photoperiods but often in other plants which took long times to head was a doubling or folding back of the rachis shown in Figure 13. It appeared that the last one or two leaf sheaths were so tightly

Figure 13. Abnormal heads of vernalized Minter wheat obtained as a result of short photoperiod treatment.
Upper photograph: (left to right) (a) Plants transferred from 11 to 18 hours at 14 weeks; (b) plants grown at 13 hours; (c) same as (a); (d) normal head from plants grown at 18 hours.
Lower photograph: Three heads at left from plants grown at 11 to 12 hours continuously; head at right from a plant grown at 18 hours continuously.



bound and perhaps lignified that the developing spikes could not force their way through. Although the cause of this abnormality is not known it appeared to occur more frequently in periods of bright sunny weather with high greenhouse temperatures. On some plants from short days there was a combination of folded rachis joints and elongated basal internodes. A few heads from these plants fell over upon emerging as shown in Figure 13.

Experiment 18 To supplement information obtained in Experiment 16 the comparative effects of long and short photoperiods were determined on spike development after initiation. Twenty-seven 6-inch pots were sown with Minter seeds which had been vernalized for 7 weeks. The pots all were held under 18-hour photoperiods in the warm greenhouse until stem elongation was evident at 36 days from planting. At this time three pots were selected at random, and the six plants were harvested for dissection. The visible leaf numbers, the numbers of spikelet primordia, the stages of development of the spikes and the spike lengths were determined. Half of the remaining pots were transferred to 11-hour photoperiods. Then at 43, 50, 57, and 63 days from planting, three pots were randomly selected from each of the two photoperiods and the plants dissected for the same measurements as were made at the first sampling. In addition, the total leaf numbers were obtained.

From the data in Table 40, it is evident that the differences in leaf numbers within photoperiods were largely due

Table 40. Further development of Minter wheat on short and long photoperiods after 36 days on long photoperiods (Experiment 18)[a]

Time of harvest (days)	Photoperiod (hrs.)	Measurements				
		Visible leaves	Total leaves	Stage[b]	Number of spikelet primordia	Spike length (mm)
36	18	6.7	-	6.5	17	4.0
43	11	7.8	8.8	7.5	16	6.0
	18	8.0	9.0	8.0	17	7.3
50	11	8.0	9.0	8.0	17	6.2
	18	8.0	9.0	8.5	15	18.7
57	11	8.0	8.0	8.0	16	12.0
	18	7.3	7.3	9.7	17	71.0
63	11	7.6	8.3	8.2	17	28.5
	18[c]	7.3	7.3	10.0	17	82.8

[a]Half of plants were transferred to 11-hour photoperiods after 36 days on 18-hour photoperiods.

[b]Stage of development of apex.

[c]Plants headed between 54 and 58 days.

to random variation and/or errors of measurement. Although some of the figures indicate an apparent decrease in leaf

numbers with increase in time, this is not likely. It is possible that there was an increase of perhaps one leaf in the plants held under short days but no large increases in leaf numbers were evident such as were found under continued short days in Experiment 16.

After the transfer of plants from long to short photoperiods there was a gradual increase in stage of development under both long and short days, but the development was much more rapid on long days. The plants on long days headed between 54 and 58 days and were all at stage 10 (completely headed) in 63 days after planting, but the short-day plants at this time were still at an average stage of 8.2 and would probably have been delayed another 2 weeks in heading if they were not harvested.

It is significant that there was no further increase in the number of spikelet primordia on either long or short days after the initial sampling at 36 days after planting. The terminal meristem had obviously differentiated to the extent of not being able to initiate new primordia.

The data on spike lengths of the plants under 18-hour photoperiods show the typical exponential growth of initiated plants on continued long days. The spike lengths of the 11-hour plants also increased exponentially but the rapid increase started at least a week later than in plants under the long photoperiods.

Thus, from Experiments 16 and 18, it can be concluded that a delay in heading by short photoperiods may appear in the form of increased leaf and spikelet numbers or a decreased rate of spikelet development and spike growth or a combination of both, depending upon when the short photoperiods are applied. When spikelet differentiation has proceeded to a certain stage the application of short photoperiods may decrease the rate of further development, but there appears to be no further increase in the leaf number. The ability of the plant to produce more leaves during early floral differentiation lies in the labile double-ridged basal primordia which, as shown by Purvis (67) with rye and McKinney and Sando (59) with wheat, may form leaves or spikelets, depending largely upon the photoperiod. After initiation has proceeded to some extent, however, the tendency for leaf production is less even on short photoperiods, and the delay seems to be largely due to effects on growth and development of the existing spikelet primordia.

Chemical Effects

Researches conducted by many workers have indicated the important modifying effects of auxins and anti-auxins on flowering (3, 7, 19, 22, 43). In several experiments conducted during 1954 and 1955, the present writer (2) found that ∝-naphthaleneacetic acid (NAA), triiodobenzoic acid (TIBA), and several other anti-auxins did not alter the

flowering response of Pawnee and Minter wheats. NAA slightly hastened the further development of spikes after initiation and resulted in a greater total number of heads per plant but appeared to have no promotive effects on initiation under short photoperiods. With reports available on the auxin-like nature of gibberellic acid[a] (GA) (12,54) it was found desirable to test this chemical on winter wheat with the hope of altering the cool temperature response or perhaps stimulating initiation under sub-optimal flowering conditions. With this objective, three experiments were conducted during the 1956-57 season. NAA and TIBA were included as comparisons in two experiments because of their typical auxin and anti-auxin characteristics.

The chemicals were applied to the foliage as a spray using a modified DeVilbis atomizer. Tergetol 7 was added to all solutions at a concentration of 0.1 per cent by volume, to facilitate wetting of the leaves. The plants were sprayed until complete coverage was obtained and the solutions started to drip from the leaves.

Experiment 11 There were indications in the literature that auxin treatments during cool temperature might accelerate heading (50). This experiment was then initiated for the purpose of testing GA. Eight 5-inch pots of each of the four

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[a]Obtained from Eli Lily Corporation

varieties, Harvest Queen, Pawnee, Minter, and Turkey, were planted on October 28, 1956. After germination and thinning the plants were held under cool temperatures (45° F. average weekly temperature) for 9 weeks. When the plants had been at the cool temperatures for 7 weeks, four pots were selected at random from each variety and sprayed with 10 ppm GA. The other four pots of each variety were held as controls. The same plants were sprayed every second day for a 2-week period, and then all the plants were transferred to the warm greenhouse and 75° to 80° F. temperatures. The plants were moved into either 14- or 18-hour photoperiod chambers. A split-plot design was used, with photoperiods as whole plots, varieties as sub-plots and chemical treatments as sub-sub-plot treatments. The experiment was replicated twice. The control and treated plants of each variety were assigned at random to the photoperiod chambers.

Measurements were made of the height of all plants at 10 and 20 days after transfer from the cool temperatures. The distance from the base of each plant to the tip of the longest leaf was measured to the nearest centimeter. The data are shown in Table 41.

At 10 days after transfer, the GA-treated plants were already 24 to 32 per cent taller than the controls under 14 hours and 6 to 27 per cent taller than controls under 18 hours. The overall plant heights at the two photoperiods

Table 41. Effects of gibberellic acid (GA) applied during vernalization of growing plants on the increase in plant height and earliness of heading of four varieties of winter wheat grown under subsequent 14- and 18-hour photoperiods at warm temperatures (Experiment 11)[a]

Variety	GA Treatment[b] (ppm)	Photoperiod (hours)	Plant height after transfer to warm temperatures: Hgt. at 10 days (cm)	Plant height after transfer to warm temperatures: Percentage control	Plant height after transfer to warm temperatures: Hgt. at 20 days	Plant height after transfer to warm temperatures: Percentage control	Time from end of cool temperature to awn emergence (days)
Harvest Queen	0	14	39		56		42
	10	14	49	126	64	114	49
	0	18	43		63		30
	10	18	50	116	76	121	35
Turkey	0	14	37		52		39
	10	14	49	132	64	123	38
	0	18	37		60		32
	10	18	47	127	66	110	27
Minter	0	14	34		45		57
	10	14	45	129	55	122	54
	0	18	41		53		33
	10	18	46	112	63	119	31
Pawnee	0	14	33		50		43
	10	14	41	124	51	102	41
	0	18	36		56		29
	10	18	38	106	60	107	30

[a]Each figure is an average of two replicates of two plants each.

[b]Treated plants received a total of seven spray applications during the last 2 weeks of cool temperatures.

differed only slightly, however. At 20 days after transfer the percentage increase in height of GA-treated plants over the controls was less in some cases than it was at 10 days. The effects of the GA treatments apparently were beginning to disappear at 20 days. Both the control and the treated plants were taller at 20 days under 18 hours than they were under 14-hour photoperiods. This was expected because the rapid initiation and spike development under 18 hours is accompanied by stem elongation.

Gibberellic acid caused increased leaf elongation as well as stem elongation in all varieties, so that both effects were included in the height determinations. Further observations indicated that the control plants had caught up with the treated plants by the time heading occurred.

Recordings also were made of the times from the end of cool temperatures to awn emergence and the data are summarized in Table 41. There were no consistent differences between the GA-treated and untreated plants over all varieties and photoperiods. As shown in Table 42, none of the chemical interactions with photoperiod or varieties were significant either. If anything, GA appeared to cause a delay in heading of Harvest Queen wheat under both photoperiods. Gibberellic acid, then, did not appear to affect floral development to any great extent even though the differences produced in plant growth were quite large for some time after treatment.

Table 42. Analysis of variance of data in Table 41 (Days to awn emergence)

Source of variation	D.f.	M.s.
Replications	1	212.70
Photoperiods (P)	1	1733.14 N.S.
Error (a)	1	61.87
Varieties (V)	3	145.47**
V x P	3	82.38*
Error (b)	6	12.97
Chemical treatments (C)	1	0.64 N.S.
C x P	1	0.93 N.S.
C x V	3	33.92 N.S.
C x V x P	3	3.87 N.S.
Error (c)	8	14.03

*Significant at 5 per cent level.

**Significant at 1 per cent level.

N.S. Not significant at 5 per cent level.

Experiment 15. It was felt that Experiment 11 would have yielded more information on the cool-temperature reactions in wheat if the cool-temperature treatments had been shorter. Therefore, in Experiment 15 the plants were treated during a sub-optimal cool-temperature treatment of 4 weeks duration. Such a treatment usually results in some acceleration of heading over warm temperature controls, but heading is still relatively delayed. In addition to GA, NAA and TIBA also were included.

Twenty-seven 5-inch pots of Minter wheat were planted on December 28, 1956, held at warm temperatures until seedling emergence and then transferred to the cool greenhouse. The pots were divided into three lots of nine and the plants thinned to two per pot. The plants remained at the cool temperatures and under 18-hour photoperiods for 4 weeks, during which time the average weekly temperature ranged from 42° to 46° F. At 15 days before the end of the 4-week period the following spray treatments were applied to the leaves: GA 50, 10, and 1 ppm, TIBA 100 and 10 ppm, and NAA 100 and 10 ppm. These treatments were randomly assigned to the pots in each of the three replications and the two remaining pots per replication were held as controls. Spray applications were made every other day for a total of seven applications, the last one ending two days before transfer of the plants to warm temperatures and 18-hour photoperiods. At the time of transfer to the warm greenhouse and for 2 days after, the leaves

were doused with water to remove any of the chemicals that adhered to the leaf surfaces. No observable growth differences were evident at the time the plants left the cool greenhouse.

Measurements were made of plant height at 7, 13, and 28 days after transfer to warm temperatures and the dates of awn emergence also were recorded. As shown in Table 43,

Table 43. Effects of gibberellic acid (GA), triiodobenzoic acid (TIBA) and ∝-naphthaleneacetic acid (NAA) applied during a 4-week cool-temperature treatment on subsequent plant height under warm temperatures and 18-hour photoperiods (Experiment 15)[a]

Chemical and concentration (ppm)	Time after transfer to warm temperatures					
	7 days		13 days		28 days	
	Height (cm)	Percentage control	Height (cm)	Percentage control	Height (cm)	Percentage control
0	27	100	41	100	55	100
GA 50	36	134	53	131	36	98
10	31	117	44	112	57	102
1	24	91	42	104	51	92
TIBA 100	20	76	37	91	49	88
10	26	99	42	104	54	97
NAA 100	24	90	40	99	57	102
10	25	92	39	95	54	97

[a]Plants were sprayed every 2 days for the last 2 weeks of the cool-temperature treatment for a total of seven applications. Each figure shown is an average of three replicates of two plants each.

plants treated with 50 and 100 ppm GA were much taller than the controls and other treatments at 7 and 13 days after transfer. The 100 ppm TIBA actually decreased plant height at all dates measured whereas 10 ppm TIBA, the NAA sprays, and 1 ppm GA appeared to have little effect. The effects of 10 and 50 ppm GA were greatest at 7 days, less noticeable at 13 days and no longer evident at 28 days. The GA applied during the cool temperatures when growth was inhibited appeared to be largely consumed in growth promotion at the warm temperatures.

The data summarized in Tables 44 and 45 on the times to awn emergence show no significant differences among the treated and untreated plants. Although the cool temperature reactions of other plants have been enhanced by GA and NAA treatments, it appears that Minter wheat is much less responsive to such treatment. In partially vernalized plants the heading variability among plants treated alike appears to be greater than any promotive effects the GA and other chemicals might have had.

Experiment 13 This experiment was designed to determine the effects of gibberellic acid on floral development in unvernalized Minter wheat. A randomized block design was used in which three concentrations of GA were applied to Minter plants at two different ages. Twenty-four 5-inch pots of Minter wheat were sown on November 23, 1956 and placed under

Table 44. Effects of gibberellic acid (GA), triiodobenzoic acid (TIBA), and α-naphthaleneacetic acid (NAA) applied during a 4-week cool-temperature treatment on the subsequent times of heading of Minter wheat at warm temperatures (Experiment 15)[a]

Treatment	Days from end of cool temperature to awn emergence[b]
Controls	81
GA 50 ppm	73
10 ppm	74
1 ppm	75
TIBA 100 ppm	75
10 ppm	78
NAA 100 ppm	78
1 ppm	82

[a]Plants were sprayed every 2 days for the last 2 weeks of the cool-temperature treatment, for a total of seven applications.

[b]Each figure is an average of three replicates of 2 plants each.

Table 45. Analysis of variance of data in Table 44

Source of variation	D.f.	M.s.
Replications	2	150.66*
Treatments	7	36.66 N.S.
Among chemicals	6	26.96 N.S.
Chemicals vs. controls	1	94.71 N.S.
Error	16	35.55

*Significant at 5 per cent level.

N.S. Not significant at 5 per cent level.

18-hour photoperiods in a greenhouse held at temperatures averaging 65° to 70° F. The plants subsequently were thinned to two per pot and the pots were divided into three replications of eight pots each. The seven treatments were assigned at random to the pots within each replication. Six of the treatments were GA applications of 1, 10, and 50 ppm concentrations made when the plants were either 6 or 10 weeks of age. The two remaining pots in each replication were held as the control treatment. Spray applications at each age were made every 4 days over a 4-week period for a total of seven applications. Therefore, half of the treated plants were sprayed with GA between 6 and 10 weeks of age, and the other half were sprayed between 10 and 14 weeks of age.

Three days following the seven spray treatments at each age, measurements were made of the plant heights and numbers of tillers. Another measurement of plant height was made 14 days after the end of the treatments and the results are shown in Table 46.

There was a positive growth response to gibberellic acid at the 10 and 50 ppm concentrations but only a 0 to 8 per cent increase in height at the 1 ppm rate. For the treatments starting at 6 weeks of age the percentage increase in plant height, over the controls, was greater at 3 days after the last spray application than it was at 14 days. With the plants which were 10 weeks old at the start of treatment,

Table 46. Effects of three levels of gibberellic acid (GA) on plant height and the production of tillers in unvernalized Minter wheat (Experiment 13)[a]

Age of plants at start of treatment	GA concentration (ppm)	Plant height after treatment				Number of tillers per plant following treatments
		Height at 3 days (cm)	Percentage control	Height at 14 days (cm)	Percentage control	
6 weeks	0	65	100	73	100	5.2
	1	70	108	75	103	4.3
	10	82	142	87	119	4.0
	50	96	148	102	140	3.0
10 weeks	0	73	100	73	100	7.0
	1	73	100	75	103	8.0
	10	78	107	83	114	6.2
	50	97	133	112	153	5.3

[a]The solutions were sprayed on the plants every 4 days for a total of seven sprays over a 28-day period.

however, there was a larger response at 14 days following the last spray application than there was at 3 days. This was due partially to the slower growth of the controls in the second age group and perhaps due also to the greater elongation of stems in the latter group.

As shown in Table 46 the number of visible tillers per plant was greatly decreased by the 50 ppm concentration of GA applied to both age groups. In the first age group, 5.2 tillers were produced by the control plants and 3.0 by the plants treated with 50 ppm GA. In the second age group, 50 ppm GA decreased the number of visible tillers an average of 2.7 per plant. The effects of 10 and 1 ppm GA were somewhat less distinct. The 10 ppm rate decreased the number of tillers of both age groups by an average of 0.8 to 1.2 per plant while 1.0 ppm GA appeared to cause a slight increase in the number of tillers of the second age group. Thus, gibberellic acid acts as a strong auxin in promoting plant growth and inhibiting tiller bud development.

A very noticeable effect of GA on the growth of wheat was a marked stimulation of stem elongation, often producing spindly plants at the higher concentrations. A typical illustration of the response to GA is shown in Figure 14. Leaves also become elongated, rather narrow and chlorotic at the higher rates of application.

Recordings also were made in Experiment 13 of the dates of awn emergence and the number of spikelets per head. The data from Tables 47 and 48 indicate that the differences in days to heading of the various GA treatments were due largely to random variability. As in past experiments with unvernalized winter wheat the variability was considerable and many

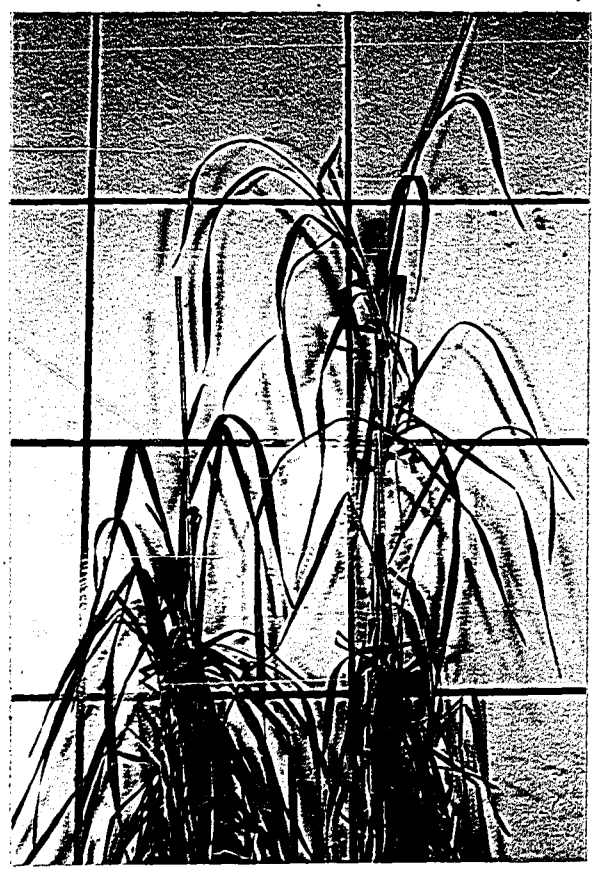


Figure 14. Effects of gibberellic acid (GA) on the growth of Minter wheat.
(left) Control plants, (right) plants sprayed 7 times with 50 ppm GA

Table 47. Effects of three levels of gibberellic acid (GA) applied to Minter wheat plants at two ages on the times to heading and the production of spikelets (Experiment 13)[a]

Age of plants at start of treatments	GA concentration (ppm)	Time from planting to awn emergence (days)	Number of spikelets per head
6 weeks	0	136	20
	1	152	21
	10	140	20
	50	138	19
10 weeks	1	146	19
	10	140	22
	50	143	15

[a]The solutions were sprayed on the plants every 4 days for a total of seven sprays over a 28-day period.

heads failed to emerge normally. The data on numbers of spikelets per head, as shown in Tables 47 and 49, fail to indicate significant differences. However, in several plants of the second age group, GA at 50 ppm caused smaller and abnormally shaped spikelets to occur. An example of this type of abnormality is shown in Figure 15 in which the spikelets have elongated but the spike length has been reduced. The number of florets per spikelet also was larger than normal.

Table 48. Analysis of variance of data in Table 47 (Days from planting to awn emergence)

Source of variation	D.f.	M.s.
Replications	2	291.27**
Treatments	6	104.85 N.S.
Error	15	38.28

**Significant at 1 per cent level.

N.S. Not significant at 5 per cent level.

Table 49. Analysis of variance of data in Table 47 (Number of spikelets per head)

Source of variation	D.f.	M.s.
Replications	2	38.323**
Treatments	6	13.116 N.S.
Error	15	5.426

**Significant at 1 per cent level.

N.S. Not significant at 5 per cent level.

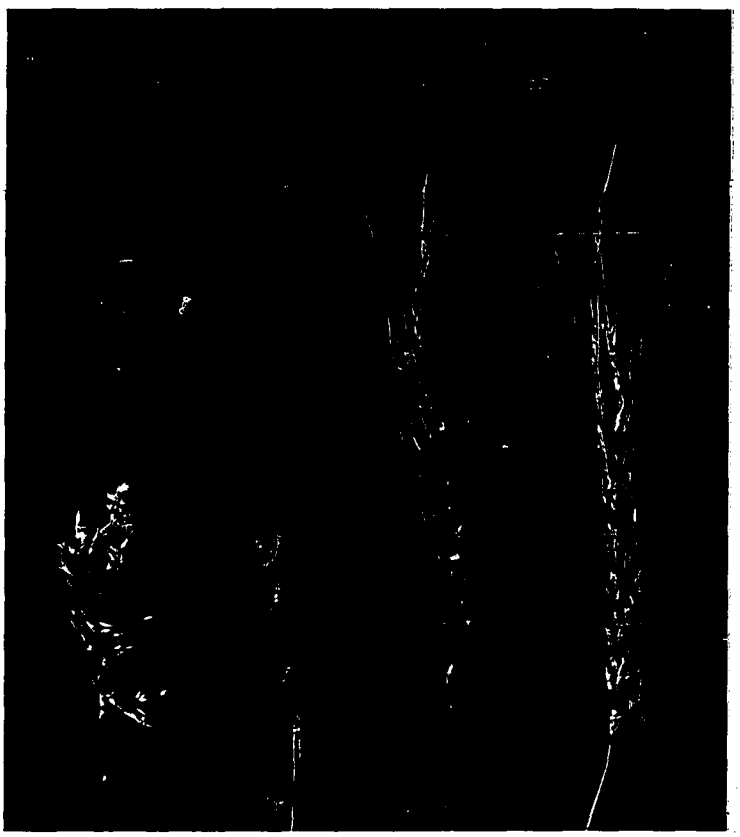


Figure 15. Effects of gibberellic acid (GA) on floral development of unvernalized Minter wheat.
Two heads on left from plants sprayed 7 times with 50 ppm GA from 10 to 14 weeks after planting, two heads on right from control plants.

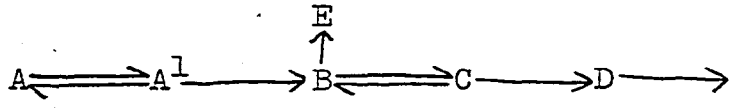
As a general conclusion on the effects of the compounds tested, it can be said that they do not appear to accelerate floral development to any extent in unvernalized plants of Minter wheat. There are no indications that either GA, TIBA, or NAA partially replaces the cool-temperature requirement as has been found in other plants. Although large growth differences were evident due to GA application, in most cases these growth differences tended to disappear when no further applications were made. In addition these large growth differences were not correlated with any promotion of floral initiation as shown in a preliminary experiment not described above.

DISCUSSION

Winter wheat differs from most biennials in that cool temperature hastens its maturity but is not essential for its eventual flowering. When planted in the spring, however, the extreme winter wheat types do not head until the following year because the growing seasons are too short and the temperatures are too high (5). Under greenhouse conditions even the extreme winter wheat types are found to be somewhat indeterminate in their temperature requirements. There are also many gradations in the temperature requirements among the winter wheats. Some varieties which require very short periods of cool temperature for early heading are grown as winter wheats, while actually they can be successfully grown from spring plantings. The varieties concerned in this study were all of the extreme winter type, which according to Dolgusin's subdivision of wheat types as reported by Wort (76) requires at least 35 to 45 days for completion of vernalization.

From the researches of McKinney and Sando (57, 58, 59) and others (42), winter wheat was classified as a short-day ⟶long-day plant with earliest flowering being obtained by cool temperatures and short photoperiods followed by warm temperatures and long photoperiods. Similar findings were obtained with winter rye (67). The most complete works on the flowering responses of winter rye have been done by Gott,

Gregory and Purvis (32), Gregory and Purvis (35, 36), Purvis (67), and Purvis and Gregory (68, 69). Gregory's group (32, 36) presented a scheme to account for the temperature and photoperiod responses in winter rye. The scheme is as follows:



where A = the precursor of the vernalization "substance"

A^1 = thermo-labile intermediate which as vernalization progresses is converted to thermo-stable B

B = precursor to flower hormones, found naturally in spring varieties of rye

C = spikelet-initiating precursor

D = spikelet-initiating hormone

E = leaf-forming hormone

The reactions between A and B represent the vernalization or thermo-induction reactions while the reactions from B on represent the photoperiodic phases of flower formation. The B to C reaction is favored by short days or darkness while the subsequent reaction C to D is favored by long days. Reactions beyond D refer to further development of the initiated spikelet primordia. Thus, if the cool reactions are included together there are thought to be at least three steps in the flowering reactions of winter rye: A to B, B to C, and C to D. These three steps are assumed to be induction,

initiation and further floral development. Much of the evidence obtained by the writer with winter wheat supports this outline of the sequences of floral reactions. It is of interest to compare, where possible, the findings in winter wheat with the evidence for the above scheme and to evaluate the scheme as a possible model for the floral development in winter wheat.

Induction

Vernalization

In an experiment conducted with leaves of Minter wheat exposed to cool temperatures (Experiment 4), it was established that the leaves alone are not effective in vernalizing the whole plant. By allowing the leaves to protrude from a heated box into air held at 40° to 50° F., it was found that no vernalization occurred in the plants during a 6-week period. It would seem that either (1) the leaves failed to carry out the cool temperature responses or (2) the vernalization product was destroyed after transport by the higher temperatures in the heated meristem. Without more information, however, a conclusion cannot be made as to whether the leaves may be receptors of the cool temperature stimulus. In the vernalizing seed, the embryo has been shown to be the locus of the cool temperature response (59) and the photoperiodic stimuli are received by the leaves (32). However, from information on bulbs and seeds it is

quite likely that the apical meristems are the loci for reception of the temperature response in the growing plant. According to Thompson (72), Chroboczek was able to show that chilling the crowns of beet plants of which the leaves and roots were exposed to warm temperatures resulted in seed-stalk formation.

The response of Minter wheat to cool temperatures is dependent upon the vernalization temperatures and duration. Vernalization at -2° C. resulted in slow germination, injury to the first foliage leaves, and no acceleration of heading, compared to the unvernalized controls under long photoperiods (Experiments 1 and 1A). In light of the experiments of Hänsel (39) with winter rye, however, it is possible that no vernalization was obtained with Minter wheat at -2° C. because the seeds were not conditioned to the freezing temperatures. Hänsel obtained vernalization at temperatures as low as -4° C. but none at lower temperatures.

The heading response to increasing durations of seed vernalization at 1° C. was not linear (Experiment 1). There in an initial lag phase of 1 to 2 weeks which results in little or no acceleration of heading of the plants grown under long photoperiods. Similar results were obtained with Minter plants and previously with Pawnee plants and seeds (2). The lag phase may involve devernalization caused by failure to reach the critical level of the cool temperature product, perhaps the thermo-labile A^1 in the scheme of Gott,

Gregory and Purvis (32). This could occur because under subsequent warm temperatures A^1 reverts to A and little or no acceleration of heading is obtained. It has been shown that devernalization occurs by high temperature following partial vernalization, but that these effects decrease as the duration of vernalization increases (69). In rye the variations from A to B are assumed to proceed autocatalytically to account for the eventual flowering of winter rye without cool temperatures. This also would appear to be the case in winter wheat as confirmed by several workers (1, 2, 42, 59).

At 1° C. a near-maximum response to increasing durations of seed vernalization was obtained in Minter wheat after about 9 weeks, and further increase in vernalization time up to 19 weeks resulted in only small but significant decreases in times to heading and in leaf number. Although not specifically determined, evidence from two experiments (Experiments 1 and 1A) indicates that a near-maximum response to cool temperature is obtained in Minter plants after 10 to 12 weeks at average weekly temperatures of 40° to 45° F. The end product of complete vernalization is assumed to be the state existing in a truly spring variety wheat which does not respond to cool temperatures. This compound or state is designated as component B in the scheme of Gott et al. (32).

Plants which received 6 weeks of cool temperature were not devernalized by a subsequent 3-week period of 90° to 100° F. temperatures in a transparent plastic chamber (Experiment 5). At the end of the 3 weeks the plants which had been in the chamber showed no lack of floral development and were not delayed in their subsequent heading times. This finding corresponds with those of Purvis and Gregory (69) who noted that devernalization decreases with increase in duration of vernalization. In terms of their scheme this meant that the thermo-labile intermediate (A^1) had reached a critical level and the thermo-stable B was produced. Other reports indicate that high temperatures after a reasonable degree of vernalization hasten floral development (14).

The summation of effects of suboptimal periods of cool temperature in Minter wheat plants appears to be possible. Plants which received a total of 6 weeks of cool temperature in either three 2-week or six 1-week alternations with warm temperatures all headed earlier than the warm temperature control plants (Experiment 2). Using comparisons among times from the end of vernalization treatments until heading, it was shown that the six 1-week periods of cool temperature were more effective than the three 2-week periods of cool temperature. It is suggested that in the case of the 2-week periods of alternating cool and warm temperatures, the plants were partially devernalized during the intermittent 2 weeks of warm periods. In the case of the 1-week alternations,

however, the cool periods were shorter, but so were the warm periods. A more extensive experiment, perhaps, with constant warm periods and varying cool periods and vise versa would help to clarify the question. The important point, however, is that partial summation of the cool temperature effects did occur.

Partial summation of cool temperature effects also occurred when the cool temperatures were applied in the seed and again in the plants after a period of warm temperature (Experiment 14). The effect of 3 weeks of seed vernalization was only partially lost during periods of 1 or 4 weeks of warm temperature before the plant vernalization treatments were applied. Lysenko reportedly supported the theory that plants or seeds could be vernalized in steps and that the sum of the effects would equal those of a continuous cool temperature treatment (44). Results with Minter wheat indicate that there is not a complete but rather a partial summation of the cool temperature effects. To determine these effects exactly would require more carefully controlled and repeatable temperature and light conditions.

Increasing durations of seed vernalization act in decreasing the leaf number as well as subsequent times to heading (Experiment 1A). Several workers have established that earliness of heading and final leaf numbers are closely related (59, 67) and that a maximum leaf number of about 25

occurs with no vernalization and short photoperiods in rye and wheat. In Minter plants grown under 18-hour photoperiods leaf numbers decreased from an average of 6.3 after 9 weeks of vernalization to 5.2 after 19 weeks of vernalization. The lowest number of leaves observed was 5. A count of the primordia after vernalization and before planting revealed 4 leaves present. Therefore, after 19 weeks of vernalization only one additional leaf was formed before spikelet initiation began. The minimum leaf number in winter wheat and rye was thought to be seven for many years, but recently Gott et al. (32) have found as few as 5 leaves in rye plants from vernalized immature seeds which contained only two to three primordia instead of the normal four. These workers suggested, therefore, that the minimal leaf concept is indeed valid; i.e., plants must lay down a minimum number of leaves before flowering.

Photoperiodic induction

With no cool-temperature treatment, plants of Minter wheat headed between 130 and 160 days on 18-hour photoperiods or in over 200 days under 11 to 15 hours (1955-56) or 11 hours (1956-57). Induction in unvernalized Turkey and Minter wheats proceeded very slowly and appeared to be relatively insensitive to photoperiod during the first 6 weeks (Experiment 8). At 10 weeks after planting no initiation was observed on any plants grown under the four photoperiods

for the first 6 weeks and 18-hour photoperiods thereafter. At 14 weeks from planting the plants were still in early stages of initiation and no trends among the induction photoperiod treatments were evident. Neither were any significant differences in heading times obtained among the plants after the induction treatments.

In Harvest Queen wheat, an 11-hour photo-induction period for 11 weeks appeared to favor initiation and development under subsequent 24-hour illumination (Experiment 8A). However, the differences were not nearly as great as those reported by McKinney and Sando (59) with the same variety. Hurd-Karrer (42) reported hastening the development of Turkey winter wheat by 2 weeks with an 8-week short-day induction period followed by long days.

Similar inductive effects of short days have been reported by other workers (32, 67, 69). Gott et al. (32) found that initiation of unvernalized rye was first observed under continuous light in 8 weeks, under 8- to 10-hour days in 12 weeks and under normal summer days in 15 weeks. The evidence for the short-day promotion of the B to C reaction in their scheme came from work with unvernalized winter rye. The present results with unvernalized Minter wheat are unfortunately inadequate to confirm these observations. It is felt that light intensity and small temperature differences play a large part in plants which receive no cool temperature treatment, for variability was quite considerable.

Large differences were obtained among the induction photoperiods in the number of tillers formed (Experiment 8). An average of about seven tillers was obtained after induction photoperiods of 11 hours and only about four tillers were produced in Turkey and Minter plants after 18-hour induction photoperiods. Short photoperiods have long been known to increase tiller production in the cereals (16, 42, 57). Differences in tillering caused by photoperiod differences have been explained on the basis of auxin concentration in the plants (47). There is evidence that more auxin is produced on long days, and that higher auxin concentrations prevent tillering (18, 47).

Both plant age and pre-treatment photoperiod affect the response to cool-temperature treatments. In general the older the plants were at the start of a cool-temperature treatment, the earlier they headed after a uniform cool-temperature treatment. Examples of this occurred in two experiments (Experiments 14 and 17). The magnitude of the differences among subsequent heading times of plants treated at different ages appears to depend upon the length of the cool temperature period. In one experiment (Experiment 14) where 2 or 4 weeks of cool temperature were applied, rather large differences were found between the times from the end of the cool temperature to awn emergence for plants treated at 1 or 4 weeks of age. However, in another experiment (Experiment

17), where plants were treated at 1, 2, 4, or 11 weeks of age for a period of 7 weeks, the differences in subsequent heading times were significant but small. In still another experiment (Experiment 3), there were no differences in subsequent times to heading among plants receiving 6 weeks of cool temperature at either 3 or 7 weeks of age. All plants in these experiments were grown on long days before the cool temperatures.

There would appear to be at least two possible explanations for such effects of plant age: (1) the increased number of tillers in the older plants increases the number of loci for the reception of the cool temperature effect, and (2) the product of the autocatalytic induction reactions at warm temperatures when added to the cool temperature induction product causes a summation effect. For the cases in which the cool temperature periods were short it would appear that (1) is a better explanation for the large differences in response to plant age. When cool-temperature treatments were longer, however, it would be expected that a large number of tillers would be produced regardless of the previous tiller number, for cool temperatures accelerate tiller production. In such a case (2) may be a better explanation. It is quite possible that both (1) and (2) are important in this regard. The production of the flower-forming precursor (B) as outlined by Gott et al. (32) would not

be expected to be great within a short time after planting since flower initiation is delayed to beyond 10 weeks in unvernalized plants. There is evidence to show that tillering is not a causal agent of flowering in wheat (59, 67), but there are no reports of the effect of tillers prior to cool-temperature treatment. This is a problem that could be solved by regulating tiller production prior to cool-temperature treatment.

Short photoperiods accelerated heading of Minter wheat in several experiments. A 4-week period of warm, 11-hour days prior to a 7-week cool-temperature treatment caused heading to occur 3 days earlier than a similar warm-temperature pre-treatment of 18-hour days (Experiment 17). In another experiment (Experiment 2), 11-hour photoperiods applied during the warm temperatures of alternating cool-temperature, warm-temperature treatments accelerated heading about 5 days as compared to 18-hour photoperiods. In two other experiments (Experiments 3 and 10) 11 hours during the cool-temperature treatments resulted in earlier heading of Minter wheat only under subsequent 11-, 13-, or 14-hour photoperiods at warm temperatures. Harvest Queen wheat showed a response similar to Minter, but Turkey and Pawnee did not. Short photoperiods during cool temperature also resulted in the formation of more spikelets per head and generally larger spikes (Experiment 10). However, when 11- or 18-hour photoperiods were applied during cool-temperature treatments

of 6 weeks duration, there was no difference in times to heading of Minter wheat under 18-hour photoperiods and warm temperatures (Experiments 2 and 3). It, therefore, appears that short photoperiods promote floral induction in Minter wheat when applied prior to or during the cool-temperature periods of moderate length even though the effects on earliness during cool temperature are masked under subsequent warm-long photoperiods. It also appears that the greater effect of short photoperiods is at the warm temperatures prior to or between cool-temperature periods. It is suggested, therefore, that the short-day photoperiodic effect is primarily through a warm temperature reaction which occurs slowly in wheat held at 40° to 48° F.

Other workers have obtained promotive effects of short days at cool temperatures in wheat or other grasses (28, 59, 65). For induction of the more determinate orchard grass, Gardner and Loomis (28) found that short photoperiods and cool temperatures could be applied separately as long as short photoperiods preceeded the cool temperatures. The reaction B to C in the scheme of Gott et al. (32) is favored by short photoperiods in unvernalized rye and would possibly account for the reactions in Minter wheat.

In two experiments where cool-temperature treatments ranging from 10 to 14 weeks in length were applied, long photoperiods accelerated heading in Harvest Queen, Minter, Pawnee, and Turkey wheats under 13-, 14-, and 18-hour days

at warm temperatures (Experiments 2 and 10). The only exceptions were in Harvest Queen and Minter wheats which were discussed above. This acceleration by 18-hour photoperiods during the cool temperatures ranged from -3 to 3 days for Minter, from -9 to 4 days for Harvest Queen, from 6 to 11 days for Turkey and from 4 to 14 days for Pawnee, depending upon the photoperiod.

From the experiments above, it was concluded that the vernalization reactions of Minter wheat are completed sometime between 6 and 10 weeks at average weekly temperatures of 40° to 45° F. Under continued cool temperatures, however, initiation of primordia is inhibited but photoperiodic reactions resulting in the initiation of primordia nevertheless proceed slowly. A similar occurrence has been observed at warm temperatures in unvernalized wheat and rye by other workers (59, 67). Purvis (67) showed that short photoperiods exert promotive effects on induction, but once the induced state has reached a maximum, further short days delay development. Thus, short days and cool temperatures are similar in their effects. The present findings in wheat do not disagree with the general findings of Purvis and Gregory (68) and Gott et al. (32) with rye, and the inductive effects of short photoperiods and cool temperatures observed thus far would appear to fit the scheme outlined.

After vernalization the varieties of winter wheat studied all headed most rapidly under the longer photoperiods

(Experiments 3, 7, 10). The general flowering response, therefore, was long-day. In Minter wheat, however, during a short period following planting of 51-day vernalized seeds, darkness or 11-hour days were equally as effective as 18-hour days when the plants were subsequently grown on continuous light (Experiment 19), A second experiment, not reported here, confirmed these results and indicated that darkness or short days for a 10-day period after planting of the vernalized seeds may actually cause slightly earlier heading than 18-hour days. Information from two other experiments (Experiments 3 and 7) in which plants were transferred from 11- to 18-hour photoperiods 2 to 3 weeks after planting the vernalized seed or after the end of a cool-temperature treatment showed that 11-hour photoperiods were more effective relative to 18-hour photoperiods during the period that immediately follows vernalization than later on.

The lack of effect of photoperiod during the short period after planting and the possible promotion by darkness indicates that a dark phase is involved in the development at this time. Until the minimum leaf number has been laid down there is thought to be an autocatalytic production of the vernalization product (34). From the above results the vernalization product would appear to be partially light-inhibited during this period of minimal leaf production. Wort (76) obtained promotion of flowering in Fulhio winter

wheat by short periods of darkness following vernalization, but Chinoy and Nanda (16) failed to obtain such a response in several Indian varieties. However, Chinoy and Nanda's exposure periods after vernalization were 12 days, which may have been too long for promotion by short days or darkness.

The idea of a dark promotion of flowering during this stage supports the scheme proposed by Gott et al. (32) for rye. The reversible B to C reaction is favored by short days and after the vernalization period, the reaction proceeds rapidly. When C has reached a critical level, however, on long days the C to D reaction will occur and spikelet initiation proceeds without delay. If short days are continued, C reverts to B, which builds up; and E, the leaf-forming hormone, is produced by the postulated B to E reaction and heading is delayed.

Several general conclusions can be made from the experiments concerning the photoperiodic-induction reactions in winter wheat. (1) The effects of photoperiod are small during 6-week induction periods with Turkey and Minter wheat. (2) Increasing plant age prior to cool temperature enhances the response to the temperature treatments. (3) Short photoperiods promote floral induction when applied during warm temperature prior to cool-temperature treatments and only slightly during cool temperatures. The photoperiodic induction phase appears to be governed by a warm-temperature, dark reaction.

Floral Initiation

All the evidence obtained in several experiments points toward the promotive effects of long days on floral initiation of Minter wheat. In plants from seeds vernalized for 9 weeks, initiation was first observed within 21 days after planting, on 18-hour days, and within 5 to 7 weeks on 11-hour days (Experiments 7 and 16). At the time of initiation the spike lengths were between 0.6 and 0.9 mm. Initiation can be assumed to be complete when the final number of spikelet primordia has been laid down and the double ridges have fused into rounded protuberances. This is attained at about stage 5 in the system used (Figure 1).

The computation of effectiveness of 11-hour photoperiods relative to that of 18-hour photoperiods was useful in showing that short photoperiods applied at the time initiation was just starting were only about 0.4 as effective as long photoperiods. Purvis (67) used a similar computation to demonstrate the time of occurrence of the condition of "ripeness to flower" in barley.

In experiments involving four photoperiods ranging from 11 to 18 hours, it was also found that the longer photoperiods invariably favored initiation, as determined by stage of development, number of spikelet primordia, and spike length (Experiments 6 and 12). Spike length and stage of development were found to be good criteria for evaluating development

while number of spikelet primordia has value over a narrower range of floral development (Experiment 7).

It can be shown in two ways that the promotion of floral initiation with increasing lengths of day is not linear. The effectiveness of 11-hour photoperiods has been shown to be about 0.4 times the effectiveness of the 18-hour photoperiods, but if the promotive effects were due to the hours of illumination received, the effect expected from an 11-hour photoperiod relative to an 18-hour photoperiod would be 11/18 or about 0.61. Obviously the true effectiveness is less than would be expected from the light received. Several experiments also have shown that there is no growth advantage in the case of 18-hour plants (Experiment 6). The photoperiodic effect also has been demonstrated by interrupting a dark period with 2 hours of light (Experiment 12). Thus, 11 + 2 hours was 94 per cent as effective as 18 hours while 13 hours was only 54 per cent as effective in promoting spikelet initiation in Minter wheat.

In addition to long photoperiods, initiation is promoted by warm temperatures. It is reported that the higher the temperature, in general, the earlier floral initiation and development occur after vernalization (14). However, it would be of interest to determine what the critical lower temperature level is for initiation in wheat. Close control of temperature would, of course, be necessary for this work.

The several experiments which involved photoperiod effects on complete floral development from planting or end of cool temperature to heading evaluated photoperiod effects on photoperiodic induction and initiation, as well as further floral development (Experiments 6, 9, 10). Since it appears that the initiation reactions are most sensitive to photoperiod and, therefore, would be most limiting, the evaluation of photoperiod effects during the entire period is largely a measure of their effects on floral initiation. Consequently, the results of such experiments were much the same as those involving initiation alone. Long photoperiods and light-interrupted dark periods accelerated heading in every case. When 11- and 18-hour photoperiods were alternated daily the effectiveness of the 11-hour photoperiods was about one-third that of 18-hour photoperiods.(Experiment 9). This value is fairly close to those obtained for photoperiod effects on initiation.

The researches of many workers attest to the promotive effects of long photoperiods in initiation of wheat and other grasses (10, 28, 42, 59, 65, 67). In the scheme of Gott et al. (32), the formation of compound C is said to occur during elongation of the apex just before double ridge formation. Then on long photoperiods the C to D reaction occurs and with increasing formation of D results in the formation of spikelet primordia from the labile double ridges. The

irreversibility of the C to D reaction is also supported by the work with Minter wheat, for very short periods of long days preceding short days always resulted in acceleration of heading compared to short days continuously.

Further Floral Development

Further floral development refers to the growth and differentiation of the spikelet primordia formed in initiation. Therefore, any study designed to evaluate effects of photoperiod on further floral development must involve the use of plants which already have initiated primordia. With the several experiments in which this was done there was only one case in which 11-hour photoperiods appeared to be as ineffective during further floral development as during initiation (Experiment 6, Part C). It is felt that this was a result of factors other than daylength, for the "effectiveness coefficients" of the 13- and 15.5-hour photoperiods in the same experiment were greater than had resulted in a comparable initiation experiment (Experiment 6, Part A).

In all other experiments, however, it appeared evident that after initiation was completed the relative effectiveness of the short photoperiods increased. The decrease in sensitivity to photoperiod seemed to coincide with the completion of initiation, when all the spikelets had started differentiation and leaf production had completely ceased. This was at stages of development between 6 and 7 and at spike

lengths of between 5 and 6 mm.(Experiment 7). There were examples of plants which headed at the same time under 11- or 18-hour photoperiods after previous initiation on long photoperiods. When this was observed the spikes had advanced to between stages 7 and 8 on long photoperiods. Several workers have reported that further floral development in different grass plants was less sensitive to photoperiod than prior stages. Wort (76) found that Marquis spring wheat was not delayed in heading on 8-hour photoperiods after 28 days of continuous illumination, but that Fulhio winter wheat required long photoperiods for the entire period to heading. Gardner (28) noted that further floral development in orchard grass was less sensitive to photoperiod than previous stages, and Purvis reported a similar situation in winter rye (67).

Under continued short days after initiation the rate of development proceeds slowly, and both the leaf number and spikelet number increases (Experiment 16). The number of primordial leaves which have only partially developed probably regulates to an extent the time of flowering after transfer to long days. When floral development has proceeded to about stage 6 on short days, however, there appears to be no further increase in leaves or spikelets, and differentiation continues under both photoperiods. However, the rate of development is more rapid on long than short days, but mainly in the early stages after the beginning of initiation (Experiment 18).

Plants which had progressed to between stages 6 and 7 on long days and were then transferred to short days were delayed in development as measured by spike length and stage of development, but the number of spikelets or leaves did not increase. Therefore, if initiation has not been completed there is a delay in heading due to both increased leaf numbers and decreased growth rates on short days, but if initiation is complete the delay is due to decreased rates of spikelet development on short days.

Stem elongation also is delayed on short days, especially in unvernalized plants on continuous short days. Fully-formed spikes may never emerge because of this inhibition of short days on elongation. Gott, Gregory, and Purvis (32) have accounted for similar occurrences in rye in their proposed scheme. The irreversibility of the C to D reaction accounts for the fact that differentiated spikelets do not revert to leaves. However, the labile double-ridged primordia are said to contain both C and D. Under short-day conditions, however, D is not formed and due to the reversible B to C reaction, E, the leaf-forming hormone, is produced and initiates new primordia at the apex. Some of the basal double ridges may, as a result, revert to leaves. Under continued short days, by autocatalytic production of B, the critical level of C is again reached and spikelet differentiation finally occurs. These explanations seem to fit the information obtained on Minter wheat. What must be kept in mind, however,

is that the scheme presented by Gott et al. (32) is merely a model to account for what is known to occur. In this way, perhaps, one will know more about what type of system to look for in any biochemical study.

The abnormal spikes produced under short or intermediate photoperiods or on long photoperiods after transfer from short photoperiods (Experiments 16 and 18) were examples of some of the many reported partial reversals of initiation under suboptimal photoperiod conditions, known as vegetative proliferation (23, 24, 25, 32, 70, 77). Wycherley's (77) explanation for vegetative proliferation was that the minimal requirement for flower initiation is greater than the requirement for culm initiation, and since the higher level is never completely reached the plant reverts to vegetative habit. In the cereals, however, the reversion involves only or or a few of the lower spikelets and not the whole spike.

Chemical Effects

From the results of two experiments (Experiments 11 and 15) in which gibberellic acid (GA), triiodobenzoic acid (TIBA), and α-naphthaleneacetic acid (NAA) were applied to wheat plants during a cool-temperature treatment, it was concluded that these compounds did not alter the flowering response. The importance of added auxins enhancing the cool-temperature effects of certain plants has been demonstrated by DeZeeuw and Leopold (19), and Lang (46). DeZeeuw and Leopold (19)

succeeded in shortening the juvenile phase normally required by Brussel sprouts before they are receptive to cool temperatures by applying lanolin pastes of NAA to the plants. Lang (46) obtained flowering in certain biennial plants by GA application in place of the normally required cool temperature. However, he was not successful in inducing unvernalized Petkus rye to head with GA applications. It may be that a different mechanism of cool-temperature responses is involved in the cereals than in some of the biennials studied.

GA also failed to promote flowering in unvernalized Minter wheat when applied every 4 days for a 4-week period starting when the plants were either 6 or 10 weeks of age (Experiment 13). Although there were no significant differences in either times to heading or numbers of spikelets produced, the 50 ppm concentration of GA applied during the 10- to 14-week period resulted in deformation of some heads and a smaller number of spikelets (Figure 15). This may have been due to an accumulation of the chemical in the leaf sheaths. Lona (53) also reported that gibberellic acid did not hasten floral initiation of winter wheat but did cause some stimulation during advanced floral development. The writer obtained promotive effects of NAA on further floral development in winter wheat in earlier work (2) as have other researchers with wheat (3) and barley (43).

Gibberellic acid applied to plants either during cool temperatures or to unvernalized plants at warm temperatures

produced remarkable growth of leaves and stems (Experiments 11, 13, and 15). A reduced number of tillers was obtained by GA applied to unvernalized wheat (Experiment 13). No growth differences were apparent at the 45° F. temperatures, but at warm temperatures there were plant height increases of up to 40 per cent over the untreated controls. As also shown by Phinney (66) with corn, however, the control plants finally grew as tall as the treated plants in the absence of further applications. The partial chlorosis in the rapidly expanding treated leaves may have been due to the distribution of a given amount of chlorophyl over larger leaf areas. The growth-promoting qualities of GA have been extensively investigated in recent years (71). From the present results GA would appear to be a strong auxin. This has been confirmed by the work of several researchers (12, 54, 66). Unfortunately it appears to have little value in flower formation of winter wheat.

SUMMARY

Studies were conducted during the fall, winter, and spring seasons of 1955-56 and 1956-57 to determine the effects of cool temperature, photoperiod, and chemical treatments on floral development of winter wheat (Triticum aestivum L.). The variety Minter was studied in detail but Harvest Queen, Turkey, and Pawnee were included in some experiments.

Cool temperature induction in Minter wheat was favored by increasing durations of vernalization in seeds or plants. Seed vernalization at -2° C. or for periods less than 1 to 2 weeks at 1° C. resulted in little or no acceleration of heading compared to unvernalized controls. A near-maximum earliness response to seed vernalization at 1° C. was attained after about 9 weeks. Increasing the time of seed vernalization to 19 weeks resulted in a minimum of five leaves being formed before heading. Maximum inductive effects of cool temperature (45° F.) in growing plants appeared to occur between 6 to 10 weeks. Plants of Minter wheat were not vernalized by exposing only the leaves to cool temperatures. Plants of Minter wheat that were vernalized for 6 weeks at average weekly temperatures of about 45° F. were not devernalized by 85° to 95° F. temperatures following.

The inductive effects of suboptimal periods of cool temperature were partially additive in Minter wheat. Increasing plant age and short photoperiods prior to cool-temperature

treatment enhanced the inductive effects and reduced times to heading after cool temperatures.

Long or short photoperiods applied to Minter wheat plants during 6 weeks of cool temperatures had no effect on subsequent times to heading under warm-long photoperiods. Under subsequent short photoperiods, however, the plants treated under cool-short photoperiod headed slightly earlier. Short photoperiods promoted induction more when applied prior to or between cool temperature periods, confirming that the short photoperiod effect is through a warm temperature reaction.

Long photoperiods applied during 10- to 14-week periods of cool-temperature treatment accelerated heading under subsequent 13-, 14-, and 18-hour warm photoperiods in Pawnee and Turkey wheats. With Harvest Queen and Minter wheats, however, cool-long photoperiods accelerated heading only under subsequent 18-hour photoperiods.

In the absence of cool temperature, photoperiods of 11, 13, 15.5, or 18 hours applied during a 6-week period resulted in no differences in the promotion of floral induction of Minter or Turkey wheats. After 11 weeks at short photoperiods, Harvest Queen plants were slightly more advanced in floral development than plants held at long photoperiods. Continued short days in both vernalized and unvernalized Minter plants greatly delayed heading, however.

Photoperiod effects were not critical for a short time after the planting of vernalized Minter seeds or just before heading. Initiation of spikelet primordia was accelerated by long days and greatly delayed on short days. The response to long days became less critical after all the primordia had been initiated. Short days after vernalization caused increases in spikelet primordia, leaf numbers, spike lengths, and numbers of tillers.

The phasic development of Minter wheat closely resembles that of winter rye and would appear to fit the sequence of reactions proposed by Gott, Gregory and Purvis (32).

Gibberellic acid did not promote induction or initiation of unvernalized winter wheat although it caused remarkable growth effects. Neither gibberellic acid, ∝-naphthaleneacetic acid, nor triiodobenzoic acid enhanced the effect of suboptimal cool temperature induction treatments.

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